UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LES EFFETS DES COUPES FORESTIÈRES SUR LA DIÈTE DES COLÉOPTÈRES EN FORÊT BORÉALE MIXTE

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
FÉLIX LONGPRÉ

SEPTEMBRE 2011

REMERCIEMENTS

Je remercie particulièrement mon directeur de maîtrise docteur Timothy T. Work, pour ses suggestions et son aide tout au long du développement et de la réalisation de ce projet de recherche. Je remercie également Éric Lucas et Frank Berninger pour leur aide au tout début du projet. Cette recherche a été financée par le Réseau de Gestion Durable des Forêts. Je voudrais donc remercier Fangliang He pour la bourse de recherche et Bruce Macnab pour la bourse de voyage. Je remercie également Daishowa-Marubeni, Canadian Forest Products et Manning Diversified Forest Products pour leurs contributions financières au projet EMEND. Merci beaucoup à Jason Edwards, Charlene Hahn et tous les autres membres de l'équipe de terrain d'EMEND pour leur aide lors de la collecte des spécimens. Merci aussi à tout le personnel du centre d'étude de la forêt ainsi qu'aux membres du laboratoire pour leur support continuel. Je voudrais également remercier chaleureusement ma famille, Annie Hibbert, Dave Gervais, Christopher O'Connor, Simon Paradis, J. Jacobs et Mélanie Desrochers pour les échanges d'idées, le support moral et tous les bons moments vécus durant ces trois années.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

La stabilité des communautés naturelles est liée aux propriétés des réseaux trophiques. Des propriétés comme l'omnivorie et le généralisme augmentent les voies possibles de transfert d'énergie et répartissent le stress de la prédation sur plusieurs espèces, se qui stabilisent les communautés, réduit la pression sur les espèces rares et minimisent la perte de biodiversité. Toutefois, la caractérisation de la diète d'organismes cryptiques comme les arthropodes épigés est complexe et requiert l'utilisation d'outils comme les isotopes stables de carbone ($\delta^{13}C$) et d'azote ($\delta^{15}N$). Le ratio isotopique du carbone retrouvé dans un organisme indique les sources d'énergie utilisé par ce dernier tandis que son ratio isotopique d'azote révèle son niveau trophique. De plus, les écarts types des $\delta^{13}C$ et $\delta^{15}N$ d'une population indiquent respectivement le degré de généralisme et d'omnivorie de cette population. Le présent mémoire présente deux chapitres sous forme d'articles. Dans le premier article, nous avons évalué les effets de divers intensités de coupes forestières en forêt boréale mixte sur le degré de généralisme et d'omnivorie de quatre prédateurs épigés (*Pterostichus adstrictus* Eschscholtz, *Staphylinus pleuralis* Leconte, *Platynus decentis* (Say), *Stereocerus haematopus* Dejean) 2, 6 et 9 ans après les coupes en mesurant la réponse isotopique ($\delta^{13}C$ et $\delta^{15}N$) des populations. Les traitements sylvicoles ont eu lieu sous deux types de couverts (feuillus et de conifères) et sont 1) des coupes totales, 2) des coupes partielles (20% de rétention) et 3) des peuplements. Toutes les combinaisons de peuplements et de traitements furent répliquées trois fois et font partie d'une expérience plus grande nommée EMEND, toujours en cours au Nord de l'Alberta. Nos résultats ont révélé peu d'effet des coupes sur le degré de généralisme et d'omnivorie des espèces. Nous avons toutefois détecté une élévation du $\delta^{15}N$ de *P. adstrictus* et *S. pleuralis* dans les coupes totales. Ces élévations du $\delta^{15}N$ pourraient indiquer des changements de diètes vers des proies de niveaux trophiques plus élevés ou encore un état de jeûne dû à un manque de ressources. Puisque les effets sont tout d'abord visibles dans les coupes totales, il est possible que les coupes partielles soient plus aptes à protéger les ressources que les coupes totales. Dans le deuxième article, nous avons testé la relation entre la longueur des coléoptères de trois guildes (herbivores, fungivores et prédateurs) et leur niveau trophique ($\delta^{15}N$). Les coléoptères furent récoltés à l'été 2000 dans les peuplements témoins de feuillus et de conifères d'EMEND. Nous n'avons pas trouvé de relation positive entre la longueur et le niveau trophique des coléoptères, mais ces résultats suggèrent que la taille détermine en grande partie la niche et le type de matière consommée par les espèces. Nos résultats démontrent également que la diète des espèces ne change pas au cours que la succession forestière, ce qui suggère une limite dans la capacité des coléoptères à changer leur type d'alimentation.

MOTS CLÉS : Isotopes stables, forêt boréale, réseaux trophiques, omnivorie, coléoptères.

INTRODUCTION GÉNÉRALE

La forêt boréale

La forêt boréale représente à elle seule 30 % des terres boisées du globe. Elle constitue l'écosystème forestier le plus septentrional de l'hémisphère nord et s'étale sur une bande de 1000 km couvrant l'Amérique du nord, la Scandinavie et la Russie. Au Canada, la forêt boréale occupe 70 % du territoire forestier et est composée principalement d'espèces de conifères et de feuillus d'intérêt commercial.

À l'échelle du paysage, la forêt boréale est une mosaïque de peuplements d'essences et d'âges différents. La composition et la réparation spatiale des peuplements sont directement liées à l'historique des perturbations ainsi qu'à la dynamique de succession végétale (Hunter, 1993 ; Messier, 1996). Les épidémies d'insectes, les chablis et les feux sont les principales perturbations naturelles capables d'initier la succession végétale en forêt boréale (Hunter, 1993). À la suite d'une perturbation majeure, les jeunes peuplements se composent d'abord d'essences feuillues à croissance rapide comme le peuplier faux tremble (*Populus tremuloides* Michx.) et le peuplier baumier (*Populus balsamifera* L.). Ultérieurement, les espèces de conifères à croissance lente et tolérant l'ombre, comme l'épinette blanche (*Picea glauca* [Moench] Voss) et l'épinette noire (*Picea mariana* [Mill.] B.S.P.) s'établiront en sous-étage. À ce stade, on qualifie le peuplement de mixte car il est dominé à la fois par des conifères et des feuillus. En l'absence de perturbation, les peuplements mixtes deviendront peu à peu (100-300 ans) des peuplements matures dominés par les conifères puisque les espèces intolérantes à l'ombre ne peuvent pas croître sous les conifères. Les différents historiques de perturbations engendrent ainsi une pluralité de peuplements forestiers distincts caractérisés par des ressources et des structures spécifiques qui jouent un rôle fondamental dans la création d'habitats et le soutien de la biodiversité (Bunnell, Kremsater and Wind, 1999 ; Hammond, Langor and Spence, 2004 ; Nordén, Appelqvist and Olausson, 2002 ; Work *et al.*, 2004).

Cependant, les avancées techniques du dernier siècle ont rendu l'industrie forestière performante à un point tel qu'elle est devenue la première source de perturbations en milieu boréal au Canada (Bergeron and Dansereau, 1993 ; Haila, 1994 ; Pratt and Urquhart, 1994).

Les méthodes traditionnelles de récolte du bois employées, comme la coupe totale, tendent à homogénéiser la structure de la forêt et peuvent à long terme occasionner une perte de biodiversité (Siitonen and Martikainen, 1994). Conséquemment, plusieurs provinces canadiennes ont adopté des lois qui encouragent les forestiers à élaborer de nouvelles techniques d'aménagements qui favorisent un développement durable de l'industrie tout en minimisant les impacts négatifs de cette dernière sur les écosystèmes (Bourgeois *et al.*, 2007).

L'aménagement écosystémique

Les écosystèmes forestiers abritent une diversité biologique prodigieuse, dont plusieurs organismes restent encore à découvrir ; il est donc impossible de planifier un aménagement forestier qui tienne compte de toutes les espèces de façon individuelle (Hansen *et al.*, 1991). Pour contrer ce problème, des chercheurs ont développé l'approche du filtre brut : une idée selon laquelle une gestion à l'échelle des écosystèmes mettant l'accent sur le maintien des différents types d'habitats et de ressources devrait permettre la survie du plus grand nombre d'espèces (Attiwill, 1994 ; Haila, 1994 ; Hansen *et al.*, 1991 ; Hunter, 1993). Partant de l'idée que les espèces sont forcément adaptées aux perturbations naturelles qui surviennent dans leur milieu, les partisans du filtre brut ont développé la notion d'aménagement basé sur les perturbations naturelles. Ainsi, un aménagement reproduisant adéquatement les effets des perturbations naturelles devrait être en mesure de conserver la biodiversité et l'intégrité d'un écosystème (Haila, 1994 ; Hansen *et al.*, 1991). Par exemple, sous cette perspective les coupes totales pourraient être utilisées afin de réamorcer le processus de succession en imitant un feu de grande intensité et les coupes partielles, en créant des ouvertures dans la canopée, pourraient entraîner les peuplements vers des stades plus avancés de la succession. L'utilisation conjointe des coupes totales et partielles pourrait donc faire en sorte que les attributs d'une forêt aménagée ressemblent d'avantage à ceux d'une forêt naturelle (Bergeron *et al.*, 1999).

L'utilisation des arthropodes comme indicateurs écologiques

Afin de déterminer si l'aménagement écosystémique préserve les structures et les ressources nécessaires à la conservation des espèces, des chercheurs ont suggéré l'utilisation de groupes d'organismes à titre d'indicateurs écologiques (Lindenmayer, Margules and Botkin, 2000 ; Noss, 1990). Un indicateur écologique est une espèce ou un assemblage d'espèces sensibles aux facteurs de stress environnementaux considérés dont la réponse est représentative d'au moins un autre sous-ensemble d'espèces présent dans l'habitat (McGeoch, 1998). Puisque les arthropodes sont très diversifiés, qu'ils prennent part à de nombreux processus écologiques, qu'ils sont sensibles aux perturbations naturelles et anthropogéniques en plus d'être aisément récoltables et entreposables à faible coût, leur utilisation à titre d'indicateur écologique en forêt boréale est encouragé par de nombreux chercheurs (Buddle *et al.*, 2006 ; Langor and Spence, 2006 ; Niemela, 1997 ; Work *et al.*, 2008).

Dans cette étude, nous porterons principalement notre attention sur les carabes (Carabidae), les staphylins (Staphylinidae) et les coléoptères saproxyliques puisque ces groupes ont utilisés afin de caractériser les effets des feux de forêts (Gandhi *et al.*, 2001 ; Holliday, 1991, 1992), des coupes totales (Buddle *et al.*, 2006 ; Heliola, Koivula and Niemela, 2001 ; Klimaszewski *et al.*, 2005 ; Koivula, Kukkonen and Niemelä, 2002 ; Niemela, Langor and Spence, 1993), des coupes partielles (Work *et al.*, 2010), des types de couverts forestiers (Work *et al.*, 2004) ainsi que pour déterminer l'impact de la qualité des débris ligneux grossiers (Jacobs, Spence and Langor, 2007).

Les études mentionnées ci-haut s'inspirent du fait que l'évaluation des effets d'une perturbation sur les communautés peut être faite en caractérisant les assemblages d'insectes avant et après la perturbation. Les différences d'assemblages observées peu de temps après la perturbation et le temps nécessaire au recouvrement des assemblages indiquent respectivement la résistance et la résilience de l'écosystème (Noss, 1990 ; Pimm, 1984). La résilience est définie comme étant la capacité d'un écosystème de recouvrer ses fonctions et structures ainsi que son taux de productivité et de biodiversité à la suite d'une perturbation, tandis que la résistance est la quantité de changement induit par la perturbation (Pimm, 1984).

À la suite d'une perturbation en forêt boréale, plusieurs changements au niveau de la température, de l'hydrologie ou des ressources alimentaires peuvent fournir des mécanismes qui expliquent directement les variations d'assemblages d'espèces. D'ailleur, les coupes forestières affectent directement la matière disponible à la base des réseaux trophiques car la récolte des arbres prive les réseaux alimentaires d'une importante source de matière végétale vivante et morte (Shaw *et al.*, 1991). Non seulement la partie aérienne des forêts contribue aux apports d'énergie nécessaires aux réseaux alimentaires, mais de nombreux organismes dépendent également de la présence des débris ligneux grossiers au sol (Hammond, Langor and Spence, 2001 ; Setälä, Haimi and Siira-Pietikäinen, 2000) lesquels sont beaucoup moins abondant dans les forêts coupées (Brais *et al.*, 2004). Ainsi, les coupes peuvent potentiellement affecter les réseaux alimentaires (Halaj *et al.*, 2005) et modifier les stratégies alimentaires des organismes (Denno and Fagan, 2003 ; Fagan *et al.*, 2002).

Les réseaux trophiques

Les réseaux trophiques demeurent au cœur de l'écologie des communautés et des écosystèmes depuis leur introduction par Elton en 1927 (Elton, 1927 ; Paine, 1980 ; Polis, 1991), ces dernier étant depuis longtemps soupçonnés d'être liés à la stabilité des communautés naturelles (MacArthur, 1955). Les réseaux trophiques sont généralement des représentations schématiques où des rectangles représentent des espèces et des flèches indiquent le sens des flux d'énergies (Paine, 1980). Toutefois, la richesse spécifique des écosystèmes est généralement si grande qu'il est souvent impossible de rendre compte de la totalité des liens trophiques présents dans une communauté (Polis, 1991). Ainsi, afin de simplifier l'élaboration et l'étude des réseaux trophiques, les guildes, qui sont des regroupements d'espèces utilisant des ressources alimentaires similaires, sont souvent utilisées (Cohen, 1989 ; Menge and Sutherland, 1987 ; Paine, 1980 ; Root, 1971). Cependant, les guildes et les niveaux trophiques discrets traditionnellement octroyés aux organismes (producteurs primaires, herbivores et prédateurs) représentent mal la réalité étant donné qu'ils ne tiennent pas compte des comportements alimentaires complexes qui diffusent les effets de la consommation sur l'ensemble du spectre trophique (Polis and Hurd, 1996).

La complexité fut initialement perçue comme ayant des effets déstabilisateurs sur les réseaux trophiques (May, 1971 ; May, 1973), alors qu'elle est maintenant reconnue comme ayant des effets stabilisateurs (Jansen and Kokkoris, 2003 ; McCann and Hastings, 1997 ; Romanuk *et al.*, 2006 ; Tilman, 1999). Parmi les comportements alimentaires qui favorisent la stabilité des réseaux trophiques grâce à la création de liens trophiques faibles, on trouve le généralisme et l'omnivorie (Fagan, 1997 ; Holyoak and Sachdev, 1998 ; McCann and Hastings, 1997 ; Polis and Strong, 1996 ; Romanuk *et al.*, 2006). Ici, le généralisme est défini comme la capacité d'un organisme à se nourrir de plusieurs espèces occupant le niveau trophique directement inférieur au sien; l'omnivorie comme étant la capacité d'un organisme à se nourrir à de multiples niveaux trophiques (Polis, 1991); et le niveau trophique comme étant : la longueur moyenne des transferts trophiques liant un organisme à la base du réseau alimentaire plus un (+1) tout en prenant en compte la contribution proportionnelle de chacun des transferts à la totalité des apports énergétiques (Yodzis, 1989). En répartissant le stress de la prédation sur plusieurs espèces, le généralisme et l'omnivorie réduisent la pression sur les espèces rares et menacées, minimisant ainsi la perte de biodiversité (Fagan, 1997 ; Holyoak and Sachdev, 1998 ; McCann, Hastings and Huxel, 1998 ; McCann, 2000 ; Romanuk *et al.*, 2006). De plus, un accroissement de la richesse spécifique permet potentiellement de stabiliser les communautés grâce à une augmentation des voies de transfert d'énergie (MacArthur, 1955). Ainsi, c'est en permettant aux organismes de consommer une multitude de ressources alternatives que l'omnivorie et le généralisme stabilisent les communautés suite aux perturbations qui entraînent une modification de la quantité ou de la qualité des ressources (Polis and Strong, 1996 ; Vadeboncoeur *et al.*, 2005). Les travaux de Romanuk ont d'ailleurs démontré que chez plusieurs espèces de zooplanctons, les populations qui ont une diète variée sont plus stables que celles qui ont une diète spécialisée (Romanuk *et al.*, 2006).

Une des formes d'omnivorie fréquemment observée chez les arthropodes terrestres est la prédation intraguilde (Mabelis, 1984 ; Polis and McCormick, 1987 ; Reichert and Cady, 1983 ; Robinson, 1987). Dans ce type de comportement alimentaire, où une espèce consomme son compétiteur, la taille de l'organisme joue un rôle déterminant, car dans la majorité des cas ce sont les plus grosses espèces qui mangent les plus petites et le niveau trophique augmente habituellement avec la taille de l'organisme (Cohen *et al.*, 1993 ; Warren and Lawton, 1987).

Ainsi, la taille des organismes peut s'avérer être un trait particulièrement intéressant lors de la modélisation de l'évolution des réseaux trophiques des arthropodes terrestres (Loeuille and Loreau, 2005).

Nous croyons que l'amélioration des connaissances sur les réseaux trophiques des arthropodes de la forêt boréale suscitera une compréhension plus approfondie des effets des différentes méthodes de coupes forestières et aidera à une meilleure planification de l'aménagement écosystémique. Toutefois, la caractérisation de la diète des arthropodes en forêt boréale est particulièrement ardue car elle nécessite l'identification des espèces au moment précis de la prédation : une tâche pratiquement irréalisable compte tenu que de nombreux arthropodes sont cryptiques, de petites tailles et qu'ils habitent souvent des milieux sombres et hétérogènes comme le sol et la litière (Eggers and Jones, 2000 ; Polis, 1991). Heureusement, les isotopes stables permettent l'étude de la diète et les comportements alimentaires des espèces sans qu'il ne soit nécessaire d'observer directement les interactions trophiques (Peterson and Fry, 1987).

Les isotopes stables

Pour un élément donné, les isotopes sont des atomes dont le nombre de neutrons diffère et on qualifie de stable les isotopes qui ne sont pas radioactifs (Fry, 2006). En nature, les isotopes légers, ceux qui contiennent le moins de neutrons, sont généralement beaucoup plus abondants que les isotopes lourds (Fry, 2006) et c'est à l'aide du spectromètre de masse qu'il est possible de déterminer le ratio isotopique (R) d'un élément dans un échantillon (R = quantité d'isotope lourd / quantité d'isotope léger). Afin de standardiser la prise des mesures isotopiques, les ratios isotopiques des échantillons sont comparés à celui d'un échantillon de référence utilisé internationalement. La valeur isotopique (δ) d'un échantillon est ensuite calculée à l'aide de la formule suivante : $\delta X = [(R_{échantillon} / R_{référence} - 1)] * 1000$. Ainsi, pour un élément donné (X), la valeur δ représente le rapport entre le ratio isotopique de l'échantillon ($R_{échantillon}$) et celui du matériel de référence ($R_{référence}$) moins un (-1) en pour mille (‰). Le matériel de référence est le PeeDee limestone pour le carbone et l'atmosphère pour l'azote (Peterson *et al.* 1987). Un δ positif signifie un enrichissement en isotopes lourds par rapport au matériel de référence alors qu'un δ négatif signifie un appauvrissement en isotopes lourds ou encore un enrichissement en isotopes légers.

Les isotopes ont des caractéristiques chimiques similaires, leurs structures électroniques étant identiques. Toutefois, leurs différentes masses atomiques entraînent des distinctions au niveau de leurs caractéristiques cinétiques et thermodynamiques (Urey 1947). Généralement, l'isotope léger exhibe des vitesses de réactions et de diffusions plus rapides que l'isotope lourd, ce qui entraîne la discrimination de l'un ou l'autre des isotopes au cours des réactions chimiques et biochimiques (Peterson and Fry, 1987). Chez les animaux par exemple, le système d'excrétion des déchets azotés favorise l'excrétion de l'azote léger. Conséquemment, la plupart des animaux sont enrichis en azote lourd par rapport à leur diète (Peterson and Fry, 1987). La différence entre la valeur isotopique d'un consommateur et sa diète se nomme fractionnement ou enrichissement (Δ) et peut être calculé avec la formule suivante : $\Delta_x = \delta X_{consommateur} - \delta X_{diète}$ (Peterson and Fry, 1987). Chez les organismes vivants, le fractionnement diffère selon la nature de l'élément, ces derniers empruntant des voies métaboliques distinctes selon leur fonction dans l'organisme. La littérature s'accorde pour dire que chez les arthropodes, l'enrichissement est de 3.4 ± 1.1‰ pour l'azote ($\delta^{15}N$) et de 0.4 ± 1.4‰ pour le carbone ($\delta^{13}C$) à chaque transfert trophique (DeNiro and Epstein, 1978, Deniro and Epstein, 1981, Gearing et al., 1984, Minagawa and Eitaro, 1984). Puisque le fractionnement est plus important pour l'azote, celui-ci permet d'évaluer le niveau trophique des espèces, alors que le carbone indique la source de nourriture à la base du réseau alimentaire (Peterson and Fry, 1987 ; Post, 2002).

Contrairement aux contenus stomacaux, qui donnent un aperçu de la diète d'un animal à un moment précis, les valeurs isotopiques (δ) reflètent la diète à long terme en nous informant de la matière qui a été intégrée aux tissus des animaux (Peterson and Fry, 1987). Lorsque les δ de plusieurs individus d'une espèce sont mesurés séparément, l'écart type des valeurs isotopiques du carbone reflète le degré de généralisme et celui de l'azote le degré d'omnivorie de la population (Márcio *et al.*, 2007 ; Romanuk *et al.*, 2006).

Les techniques modernes de spectrométrie de masse permettent désormais de déterminer simultanément les ratios isotopiques du carbone et de l'azote contenus dans un échantillon sans que cela ne nécessite de manipulations ou de coûts supplémentaires. Ainsi, les isotopes stables d'azote et de carbone sont devenus des outils de prédilection pour l'étude des réseaux trophiques des sols (Chahartaghi *et al.*, 2005 ; Setälä and Aarnio, 2002), des milieux

aquatiques (Atshusi and Yoshito, 2005 ; Hansson and Tranvik, 2003 ; Romanuk *et al.*, 2006), agricoles (Albers, Schaefer and Scheu, 2006 ; McNabb, Halaj and Wise, 2001) et forestiers (Bennett and Hobson, 2009 ; Halaj, Peck and Niwa, 2005 ; Ponsard and Arditi, 2000 ; Scheu and Falca, 2000).

En milieu forestier, les valeurs isotopiques du carbone et de l'azote ont révélé la présence de plusieurs groupes trophiques (Ponsard and Arditi, 2000 ; Scheu and Falca, 2000). En constatant que les valeurs isotopiques des différents groupes trophiques constituent un continuum plutôt que des groupes avec des frontières précises, ces mêmes études ont donc confirmé l'importance de l'omnivorie chez les insectes forestiers (Ponsard and Arditi, 2000 ; Scheu and Falca, 2000). De plus, les travaux de Bennett et Hobson ont démontré qu'en forêt boréale, les groupes d'insectes spécialistes, comme les orthoptères, exhibent moins de variabilité isotopique que les groupes d'insectes généralistes comme les carabes (Bennett and Hobson, 2009). Les études mentionnées ci-haut ont toutes eu lieu dans des forêts non perturbées. À notre connaissance, la seule étude utilisant des isotopes stables en milieu perturbé est celle de Halaj (2005). Cette étude suggère la présence de deux à trois niveaux trophiques chez les arthropodes forestiers, l'existence de beaucoup de prédation intraguilde et démontre qu'après 17 et 42 ans, les éclaircies forestières n'ont pas d'effets détectables sur la signature isotopique des d'arthropodes (Halaj, Peck and Niwa, 2005). À ce jour, les études isotopiques sur les arthropodes forestiers sont donc généralement descriptives et effectuées au niveau de l'ordre ou de la famille.

Nous sommes persuadés que l'étude des effets des coupes forestières sur les réseaux trophiques des arthropodes permettra une meilleure compréhension des changements observés chez communautés d'arthropodes suite aux perturbations anthropogéniques. Ainsi, le présent mémoire comprend deux chapitres sous forme d'articles présentant les résultats de nos recherches sur les effets des coupes forestières sur la diète des coléoptères dans un contexte d'aménagement écosystémique. Le premier article présente les résultats d'une expérience sur l'effet de la sévérité des coupes forestières, du couvert forestier et du temps écoulé depuis les coupes sur la nature et la variabilité de la diète de 4 coléoptères de la forêt boréale. Le deuxième article présente les résultats d'une expérience étudiant les liens entre la

grosseur des coléoptères et leurs niveaux trophiques ainsi qu'une caractérisation des valeurs isotopiques de plusieurs autres coléoptères saproxyliques dans des peuplements non-coupés.

Le site d'étude

Notre site d'étude se trouve au Canada dans le nord-ouest de l'Alberta sur le territoire du projet de recherche EMEND (Ecosystem Management Emulating Natural Disturbance) : l'une des plus importantes expériences ayant pour but la caractérisation à long terme des effets de l'aménagement écosystémique sur la faune, la flore et la productivité des différents peuplements de la forêt boréale (Spence, Volney, 1999). Le projet EMEND s'étend sur une aire de 24 Km^2 dans l'écorégion des Lower Foothills au nord-ouest de Dixonville (56°46'13''N, 118°22'28''W) (Work *et al.*, 2004) à une altitude allant de 667 à 880 mètres. Les sols y sont relativement riches avec une texture lacustre fine (Kishchuk, 2004) et les coupes furent effectuées durant l'hiver de 1998 et 1999. Le secteur est caractéristique de la forêt boréale mixte de l'ouest et dominé par les espèces d'arbres suivantes : *Populus tremuloides* Michaux (peuplier faux tremble), *Populus balsamifera* L. (peuplier baumier), *Picea glauca* (Moench) Voss (épinette blanche), *Picea marianna* Miller (épinette noir) et *Abies balsamea* (Linné) Miller (sapin baumier). Le dispositif expérimental en place à EMEND comporte deux facteurs : le type de couvert forestier et le taux de rétention des coupes. Chaque combinaison de facteurs fut répliquée trois fois dans des parcelles expérimentales de 10 acres nommées compartiments et on y trouve 4 types de couverts forestiers et 5 niveaux de rétention en plus des compartiments témoins non-coupés.

Premier chapitre

Notre premier chapitre traite des effets à long terme de l'intensité des coupes et du type de couvert forestier sur la diète de 3 espèces de carabes et d'une espèce de staphylinae communément récoltés dans la région. Nous avons utilisé des insectes (conservées dans l'éthanol) récoltés en 2000 et 2004 lors de projets antérieurs ainsi qu'une collection que nous avions effectuée durant l'été 2007. Les travaux de Sarakinos ont démontré que les spécimens conservés dans l'éthanol sont utilisables à des fins de recherches isotopiques (Sarakinos *et al.*, 2002). Puisque l'écart type des valeurs isotopiques augmente proportionnellement à la

variabilité intraspécifique des niveaux trophiques et des types de ressources consommées par la population étudiée (Márcio *et al.* 2007, Ponsard *et al.* 2000, Romanuk *et al.* 2006), nous avons mesuré la variabilité de la diète au niveau de la population et non au niveau de l'individu. Ainsi, les variables réponses utilisées pour cette étude sont la moyenne et l'écart type des $\delta^{13}C$ et $\delta^{15}N$ des espèces au niveau du compartiment (n=3). Les moyennes et les écarts types des δ des compartiments ont été calculés à partir de 7 spécimens mesurés individuellement (sauf si mention) pour chaque espèce. Nous avons ensuite considéré trois facteurs : 1) le temps écoulé depuis les coupes, 2) l'intensité des coupes et 3) le type de couvert forestier. Pour le facteur temps, nous avons mesuré les δ de spécimens récoltés la deuxième, sixième et neuvième année après les coupes. En ce qui a trait à l'intensité des coupes et aux types de couverts, nous avons retenu trois niveaux de rétention et deux types de couverts, soit les peuplements contrôles (non-coupés), les coupes partielles (20 % de rétention) et les coupes totales (0-2 % de rétention) dans les peuplements composés à plus de 70 % de feuillus (DDOM) ou de conifères (CDOM).

Nous avons testé les 3 hypothèses suivantes : 1) l'écart type des valeurs isotopiques sera plus grand dans les coupes totales que dans les traitements contrôles et les coupes partielles (20 %) exhiberont des résultats intermédiaires ; 2) l'écart type des valeurs isotopiques observées diminuera avec le temps pour l'ensemble des espèces étudiées et 3) les valeurs isotopiques avec des écarts types seront moins grands dans les peuplements coupés (0 % et 20 %) dominés par le tremble que dans ceux dominés par l'épinette. Ces hypothèses précédentes nous ont permis de déterminer empiriquement si les espèces généralistes ajustent leurs comportements et manifestent plus de variabilité alimentaire dans les milieux les plus perturbés.

Deuxième chapitre

Le deuxième chapitre, traite des liens entre la longueur des coléoptères et leurs niveaux trophiques, en plus de caractériser les valeurs isotopiques de plusieurs espèces de carabes, de staphylins et de coléoptères saproxyliques des peuplements témoins pour l'été 2000. Nous avons testé les hypothèses suivantes : 1) le niveau trophique des coléoptères augmentera avec leur grosseur chez les prédateurs et non chez les herbivores et les fungivores; 2) les valeurs de $\delta^{15}N$ des herbivores seront les plus basses suivies de celles des fungivores et des prédateurs; 3) à l'intérieur même des guildes, les valeurs isotopiques de $\delta^{15}N$ des espèces s'étalleront sur un continuum de valeur.

En établissant les bases nécessaires à un approfondissement des connaissances des réseaux alimentaires des arthropodes d'EMEND, nos recherches permettront une meilleure compréhension des mécanismes responsable de la réponse des coléoptères à l'aménagement écosystémique et pourrons aider au perfectionnment de ce dernier.

CHAPITRE I

STABLE ISOTOPE ANALYSIS OF FOREST BEETLES REVEAL LIMITED CHANGES IN OMNIVORY AND GENERALIST FEEDING FOLLOWING PARTIAL AND CLEAR CUT HARVESTING

Félix Longpré and Timothy T. Work

Félix Longpré was responsible for the planning, field work, identification of specimens, compiling of data and analysis. Timothy T. Work contributed as director throughout all stages and co-author of the article. Funding was provided in part by a SFMN grant awarded to Fangliang He (University of Alberta). This article is ready for submission to Oecologia.

1.1 Abstract

Increasing diet breadth either within or across trophic levels can facilitate recovery of species and in some cases communities following perturbation. Changes in diet breadth or diet shifts within a trophic level can be characterized in terms of isotopic carbon ($\delta^{13}C$), while trophic shifts or increasing omnivory can be characterized in terms if ($\delta^{15}N$). We compared whole body $\delta^{13}C$ and $\delta^{15}N$ to evaluate whether feeding behavior of four litter-dwelling predators: *Pterostichus adstrictus, Staphylinus pleuralis, Platynus decentis, Stereocerus haematopus* changed in response to forest harvesting and forest cover 2, 6 and 9 years following harvest in boreal mixedwood forests of Western Canada. Beetles were collected from replicated stands which were 1) clear cut, 2) harvested through partial cutting leaving 20% dispersed retention and 3) uncut in 1999-2000 as part of the a larger experiment called EMEND. Specifically we tested whether increasing levels of harvest provoked increased generalist feeding within a trophic level or omnivory in beetles. We found little evidence of harvest induced changes in generalism and omnivorous in these species. However, we found that *P. adstrictus* and *S. pleuralis* had elevated $\delta^{15}N$ in clear cuts. These increases could be attributed with either a shift towards prey with elevated $\delta^{15}N$ or a starvation response related to a lack of available prey. The fact that shifts towards higher levels of $\delta^{15}N$ are limited to clear-cuts also suggest that partial cutting may maintain underlying resources needed for higher trophic levels better than more intensive level of harvesting.

Keywords: Stable isotopes, Boreal forest, Food webs, omnivory, generalist predators, Carabidae, Staphylinidae.

1.2 Introduction

Omnivory, feeding at multiple trophic levels, and generalist feeding within a trophic level are considered stabilizing factors in food webs which favor the capacity of communities to recover following disturbance (Fagan, 1997 ; McCann and Hastings, 1997 ; Polis, 1991 ; Romanuk *et al.*, 2006). In this context, prey switching by omnivores and generalist predators may buffer changes in lower trophic level consumers that occur following perturbation (Odum, 1953). Distributing the effects of predation among many potential prey species, may also have an indirect benefit for maintaining biodiversity particularly if predation risks are reduced on rare or declining prey species (Fagan, 1997 ; Holyoak and Sachdev, 1998 ; McCann *et al.*, 1998 ; McCann, 2000 ; Romanuk *et al.*, 2006).

Soil and litter food webs are replete with omnivory and other complex interactions (Moore *et al.*, 2004). These food webs are often comprised of large numbers of cryptic organisms in inaccessible habitats which severely limits the potential for direct observation of feeding behaviors (Polis, 1991). Use of stable isotopes permits reconstruction of feeding strategies and resource use within food webs as stable isotope values (SIV) of organisms reflect those of their diet (Peterson and Fry, 1987 ; Post, 2002). SIV have been widely used to characterize food webs in both terrestrial (Bennett and Hobson, 2009 ; Blüthgen, Gebauer and Fiedler, 2003) and aquatic systems (Hamilton *et al.*, 2004 ; Paetzold, Schubert and Tockner, 2005) as well as the interface between these systems (Gratton and Vander Zanden, 2009 ; Kupfer *et al.*, 2006). They have proved useful in the evaluation of anthropogenic disturbance impacts such as forest harvesting (Nakagawa *et al.*, 2007) and habitat fragmentation (Layman *et al.*, 2007). These techniques have been used extensively particularly in the study of arthropod food webs (Halaj, Peck and Niwa, 2005 ; McNabb, Halaj and Wise, 2001 ; Ponsard and Arditi, 2000 ; Wise, Moldenhauer and Halaj, 2006) and soil communities (Scheu and Falca, 2000 ; Scheu and Folger, 2004). In uncut forests, stable isotopes have been used to study arthropod food webs by the characterization of general trophic groups like predators and detritivores (Bennett and Hobson, 2009 ; Ponsard and Arditi, 2000 ; Scheu and Falca, 2000).

The difference in SIV between consumers and their food source is termed fractionation (Δ) (Post, 2002). Nitrogen and carbon fractionation values for one trophic level are 3.4 $\pm$

1.1‰ and 0.4 ± 1.4‰ respectively (DeNiro and Epstein, 1978, 1981 ; Minagawa and Eitaro, 1984). Because nitrogen isotopic values ($\delta^{15}N$) increase or fractionate appreciably with each trophic level they are often used to determine the trophic position of organisms (Post, 2002). Carbon isotopic values ($\delta^{13}C$) are comparably less sensitive to changes in trophic levels and are used to identify major differences in carbon sources at the base of a food chain (Post, 2002). In this context, standard deviations of $\delta^{13}N$ and $\delta^{15}C$ can be used as proxies of omnivory and generalist feeding respectively within populations (Romanuk *et al.*, 2006). Hence, a population where individuals feed across multiple trophic levels will yield higher standard deviation in terms of $\delta^{15}N$ as compared to a population where individuals feed at the same trophic level. Romanuk et al. (2006) found populations to be more stable when they exhibited higher standard deviations of $\delta^{13}C$ and therefore more generalist feeding further suggesting that feeding behaviors could be linked to population resilience after a disturbance event.

In boreal forests, harvesting has become an important disturbance event which in some cases affects a larger cumulative area than natural disturbances such as wildfire (Pratt and Urquhart, 1994). Forest harvesting is known to alter plant and animal abundance and composition at least initially (Drapeau *et al.*, 2003 ; Heliola, Koivula and Niemela, 2001 ; Koivula, Kukkonen and Niemelä, 2002 ; Macdonald and Fenniak, 2007 ; Work *et al.*, 2010) which may in turn alter resources, food webs and trophic interactions. To minimize impacts on diversity, management strategies that emulate natural disturbances and coarse filter approaches to conservation have been proposed (Armstrong *et al.*, 2003 ; Attiwill, 1994 ; Bergeron and Harvey, 1997 ; Lindenmayer, 1999 ; McLaren, Thompson and Baker, 1998 ; Noss, 1999 ; Spence, 2001). The coarse filter approach advocates that habitat conservation is an efficient way to preserve most species when it is impractical to account for each species individually (Attiwill, 1994; Hunter, Jacobson and Webb, 1988). In this context, less intensive silvicultural approaches such as partial cutting which retain standing forest structure are currently being implemented and evaluated in terms of their effects on biodiversity (Martikainen, Kouki and Heikkala, 2006 ; Work *et al.*, 2010 ; Work *et al.*, 2008). The coarse filter perspective is based fundamentally on the premise that long-term associations and adaptations of organisms to natural disturbances. The degree to which organisms are capable

of shifting or expanding dietary preferences in the face of disturbance will arguably affect their persistence following forest harvesting as well as the need for coarse-filter strategies.

Here we compared SIV of dominant boreal beetle species collected 2, 6 and 9-years following experimental, partial-cutting treatments to determine whether increasing levels of harvesting influenced the degree of omnivory and generalist feeding. We expected omnivory and generalist feeding would increase with intensity of harvest based on the assumption that increasingly severe disturbances will have relatively larger effects on lower trophic levels and resources. We also expected that initially carbon sources, and thus $\delta^{13}C$, would differ for species collected in deciduous versus conifer dominated stands (Brooks *et al.*, 1997; Schulze, Chapini and Gebauer, 1994). We expected that this initial difference in $\delta^{13}C$ would be lessened in harvested stands as deciduous regeneration returns in both deciduous and coniferous stand-types and will continue to decrease with time since harvest (Armstrong, 1999; Work *et al.*, 2010).

1.3 Methodology

1.3.1 Study site

Our study took place in the Lower Foothills ecoregion of Alberta, Canada at the Ecosystem Disturbance Management Emulating Natural Disturbance (EMEND) experimental site (56°46'13''N, 118°22'28''W). The site covers 24 km² and ranges in altitude between 667 and 880 m (Work *et al.*, 2004) and has relatively rich, lacustran soils (Kishchuk, 2004). The site is characteristic of western boreal mixed forest and is dominated by trembling aspen (*Populus tremuloides* Mich.), balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea marianna* Mill.) and balsam fir (*Abies balsamea* (L.) Mill.). EMEND is a long-term, manipulative experiment, where whole stands from four dominant cover types were subjected to 6 levels of variable retention harvesting in a randomized complete block design (Spence, Volney, 1999). All treatment by cover-type combinations were randomly assigned to 10 ha experimental units (further referred to as compartments) and replicated three times. Harvesting took place during the winter of 1998-1999, trees were delimbed near the road at the compartment limit and piles were burned on

site. All stands were between 80 and 140 years of age and had never been commercially harvested prior to the establishment of the EMEND project (Spence, Volney, 1999).

For this experiment, we used insects collected from deciduous dominated [DDOM] and conifer dominated [CDOM] stands-types. DDOM stands were composed of >70% *P. tremuloides* and *P. balsamifera* while CDOM stands were composed of >70% *P. glauca* and *P. marianna* prior to harvest. These stand types represent the earliest and latest stages of boreal mixedwood succession in this region (Lieffers *et al.*, 1996). In 1998-1999 a series of harvesting treatments were applied throughout the site. For our study we used clear-cuts (0%), partial cuts (20% residual) and uncut control blocks (100%). We analyzed SIV from insects collected 2 (2000), 6 (2004) and 9 (2009) years after harvest.

1.3.2 Arthropod sampling

We have focused our efforts on species that responded to forest harvesting treatments but were present in sufficient numbers to properly evaluate isotopic means and standard deviations throughout 2000-2007. We targeted four of the largest and most abundant species of predatory beetles. These were three carabid species: *Pterostichus adstrictus* Eschscholtz, *Platynus decentis* (Say) and *Stereocerus haematopus* Dejean; and one staphynilid: *Staphylinus pleuralis* Leconte. *P. adstrictus* and *S. pleuralis* were collected in both cover types, while *P. decentis* and *S.haematopus* were only collected in DDOM and CDOM compartments respectively.

For the 2nd and 6th year following harvest, we used preserved specimens from previous pitfall trap collections (Work *et al.*, 2004). These specimens were collected from permanent sampling plots set-up throughout each compartment. When found in sufficient numbers, we took all seven specimens from a single trap and collection date, otherwise multiple collection dates and traps were combined although pooled samples always represented a single experimental stand. In 2007, target species were collected by pitfall trapping and hand collecting. Between ten and twenty pitfall traps were randomly placed within experimental compartments, filled with salt saturated water and collected every 4 days. Samples were frozen prior to processing. All specimens used in this study were identified to species with taxonomic keys developed by C. Lindroth (Lindroth 1966). In order obtain a wider view of

the food web, we also collected leaf litter and vegtation (both deciduous and coniferous), herbivore species (Lepidopteran larvae and Acrididae), spiders (Lycosidae), carrion beetles (Silphinae) and shrews in 2007. Vegetation samples were randomly collected within a 10 meter radius around pitfall traps and dried prior to preparation for combustion in the mass spectrometer.

1.3.3 Stable isotope content

Specimens were rinsed with distilled water and freeze dried in a Freezone 12 lyophiliser (Labconco^{TM}, Kansas City, MO, USA). We ground whole specimens with a mortar and pestle and encapsulated subsamples of 0.6 to 0.8 µg in tin cups. We used a mass spectrometer (Micromass IsoPrime GVI, Manchester, UK) to measure $\delta^{13}C$ and $\delta^{15}N$ values (Post, 2002). $\delta^{13}C$ and $\delta^{15}N$ are expressed in per mil (‰) and are calculated with the following formula: $\delta E = [(Rsample / Rstandard - 1)] * 1000$ where E is the element and R is the ratio of heavy to light isotope ($R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$) of the sample and the standard material. We used PeeDee limestone as a standard for carbon and air as for nitrogen (Peterson and Fry, 1987). Raw data was corrected with a calibration curve based on two reference materials: leucine ($\delta^{13}C$=-28,50‰; $\delta^{15}N$=-0,26‰) and DORM-2 ($\delta^{13}C$=-17,35‰; $\delta^{15}N$=+14,36‰).

1.3.4 Data analysis

We measured carbon and nitrogen isotopic values of 888 insect specimens: 272 *P. adstrictus*, 308 *S. pleuralis*, 119 *S. haematopus* and 147 *P. decentis*. We used compartment level means and standard deviations of insect $\delta^{13}C$ and $\delta^{15}N$ as response variables. In every compartment and for each species, isotopic values of up to 7 specimens were used to calculate the $\delta^{13}C$ and $\delta^{15}N$ means and standard deviations. We used linear mixed models to test the hypotheses that intensity of harvesting and time since disturbance influence trophic position as well as omnivorous and generalist feeding in our species (Pinheiro and Bates, 2005). We produced species-specific, sequential ANOVA models where cover type, harvest intensity, time since harvest and their interactions were defined as fixed effects and compartment was defined as a random effect with independent intercepts. Normality and homogeneity of variance were confirmed by the examination of normal quantile-quantile

plots and fitted vs observed plots for all models (Pinheiro and Bates, 2005). All statistical tests and figures were made using R 2.7.0 (R Development Core Team 2007) and the "nlme" package (Pinheiro and Bates, 2005).

1.4 Results

1.4.1 Global model

For all species, $\delta^{15}N$ values spanned approximately one trophic level ($\approx$ 3.4‰). S. *haematopus* had the highest $\delta^{15}N$ values followed by *P. adstrictus* and *S. pleuralis*. *P. decentis* had the lowest $\delta^{15}N$.

1.4.3 Harvesting effects

$\delta^{15}N$ varied by cover-type ($F_{1, 12} = 5.96$, $p = 0.0311$) for *P. adstrictus* (Figure 1.1) and this difference was equivalent to 3% of a trophic level (0.1‰). The $\delta^{15}N$ of *P. adstrictus* and *S. pleuralis* was significantly (or near significantly) affected by harvesting intensity ($F_{2, 12}$ =4.81, p=0.0293 and $F_{2, 12} = 3.55$, $p = 0.0616$, respectively) regardless of cover type with highest $\delta^{15}N$ values being found in clear-cuts for both beetle species (Figure 1.1). Of the species that were collected from both cover-types, *P. adstrictus* and *S. pleuralis*, had increased $\delta^{13}C$ in conifer habitats (CDOM) compared to deciduous (DDOM) habitats ($F_{1, 12} = 31.96$, $p < 0.0001$ and $F_{1, 12} = 27.68$, $p = 0.0002$, respectively) (Table 1.1, Figure 1.1).

We observed no differences in the SD of $\delta^{15}N$ save a significant effect of time since harvest in *P. decentis* ($F_{2,10} = 5.23$, $p = 0.0311$) for which we observed a decrease in the SD of $\delta^{15}N$ in 2004 (Figure 1.2).

1.4.4 Time since harvest effects

Temporal differences in $\delta^{15}N$ were significant for all species with the exception of *S. haematopus* (Figure 1.3). We observed a significant time by cover-type interaction in $\delta^{13}C$ for *P. adstrictus* ($F_{2, 23} = 5.27$, $p = 0.0130$) where differences between CDOM and DDOM stands decreased with time (Figure 1.3). Interannual variation of $\delta^{13}C$ was significant for *P. decentis* in DDOM stands ($F_{2, 10} = 18.65$, $p = 0.0004$) and *S. haematopus* in CDOM stands ($F_{2, 8}$ =

8.08, p = 0.0120) with the highest $\delta^{13}C$ values found 6 years after harvest in both species (Figure 1.3).

We observed yearly differences in SD of $\delta^{13}C$ for *P. adstrictus* and *S. haematopus* ($F_{2,20}$ = 5.41, p = 0.0132 and $F_{1,3}$ = 34.04, p = 0.0100, respectively). $\delta^{13}C$ variation was lowest in 2004 in both species (Figure 1.4). Furthermore, we have observed a significant interaction between year and treatment in the SD of $\delta^{13}C$ for *S. haematopus* ($F_{2,3}$= 42.63, p = 0.0063) where the SD of $\delta^{13}C$ in the clear cuts increased with time contrary to the other treatments. Because of missing data year 2007 had been excluded from this analysis.

1.4.5 Reference taxa

In 2007 $\delta^{15}N$ of reference taxa remained similar throughout all retention treatments (Figure 1.5). Plant material constantly exhibits the lowest $\delta^{15}N$ values followed by the herbivores (Lepidopteran larvae and Acrididae), the predators, the carrion beetles and the shrews (figure 1.5).

1.5 Discussion

1.5.1 Stand-type differences

Species collected in deciduous stands had a lower SIV for C (≈ -1.5‰) than those collected in conifer stands suggesting that the base carbon sources for these stand-types differ. These observed values are consistent with those reported for white spruce (–26.5±0.72‰) and trembling aspen (–28.0±0.79‰) by Brooks *et al.* in 1997, suggesting that tree species composition affects food webs up to the level of predators. Furthermore, consistent differences in C among stand types imply that these species and their prey do not feed in different stand-types, indicating that their 'realized' dispersal may be limited.

How quickly a change in tree composition affects isotopic signatures is not yet clear. After a major natural or anthropogenic disturbance in mixedwood boreal forests, the first cohort of trees are usually fast growing shade intolerant deciduous species (i.e. trembling aspen) (Bergeron and Harvey, 1997 ; Lieffers *et al.*, 1996). Likewise, corresponding changes in boreal coleoptera communities following harvesting and other disturbances are often closely related to time since disturbance (Buddle *et al.*, 2006 ; Koivula, Kukkonen and

Niemelä, 2002 ; Niemela, Langor and Spence, 1993 ; Work *et al.*, 2010). We expected that $\delta^{13}C$ of beetles in conifer stands would become increasingly similar to those from aspen stands as conifer leaf litter was replaced by the deciduous leaf litter produced by the regenerating aspen cohort within the cut stand. However, without clear interactions between cover type, year and treatment on isotopic carbon or nitrogen, we cannot conclude that the time related effects are the result of forest regeneration and the establishment of deciduous species in conifer stands. Further investigations will be needed to understand the nature of the factors that explained these experiment wide effects.

1.5.2. Trophic interactions

The observed range of $\delta^{15}N$ values for these four species spans an entire trophic level (3.4‰). These results are consistent with findings of Ponsard and Arditi (2000) and Scheu and Falca (2000) who demonstrated that $\delta^{15}N$ values of detritivores and predators in forest soil food webs span at least one trophic. We were also able to observe finer scale, species-specific differences within the generalist predator guild (i.e. *P. decentis* consistently exhibited the lowest $\delta^{15}N$; while, *S. haematopus* exhibited $\delta^{15}N$ value about one trophic level higher). This supports a well-established perspective that within guilds, the species' feeding preferences constitute continuums of $\delta^{15}N$ rather than fixed and discrete trophic levels (Hishi *et al.*, 2007; Ponsard and Arditi, 2000 ; Scheu and Falca, 2000).

Interestingly, for both species whose $\delta^{15}N$ was affected by harvesting intensity (*P. adstictus* and *S. pleuralis*), clear-cut yielded the highest $\delta^{15}N$ values while the controls and 20% residual stands yielded similar values. Differences in $\delta^{15}N$ related harvesting did not exceed 0.54‰ (about 16% of a trophic level). There are two different explanations possible for this effect. The first suggests that in clear cuts *P. adstrictus* and *S. pleuralis* consumed prey at a higher trophic position and signifies a shift in diet. The second explanation suggests enrichment of $\delta^{15}N$ resulted due to a starvation response by which individuals auto-cannibalize their own tissues. Such enrichments due to starvation have been well documented in arthropods (Haubert *et al.*, 2005 ; Oelbermann and Scheu, 2002) and are of the same magnitude of $\delta^{15}N$ values found in our study. Furthermore, oribatid mites which contribute to the base of the food web have been show to decrease in clearcuts (Lindo, 2004). The

'starvation' hypothesis is consistent with a collapse of *P. adstrictus* in the aspen dominated compartment 4 year after the clear cuts (Jacobs, Work and Spence, 2008). It is also possible that a mix of the two explanations discussed above occurred: *P. adstrictus* could have been starving in the DDOM clear cuts while feeding on higher trophic level in the CDOM clear cuts.

Increased $\delta^{15}N$ limited to clear cuts also suggest that partial cutting may maintain underlying resources needed for higher trophic levels better than more intensive methods of harvesting. Similar, results have been reported elsewhere. Halaj (2005) reported no significant $\delta^{15}N$ increase in broad arthropod groups collected from thinned stands (Halaj, Peck and Niwa, 2005). Furthermore, the 2007 results obtained with other taxa groups shown in figure 1.5, suggest these effects may be species specific and that treatment related trophic shifts did not occur in the rest of the assemblage.

1.5.3. Omnivory and generality

Others have suggested that omnivory and generalism help stabilize both communities and populations (Romanuk *et al.*, 2006) particularly following disturbance (Fagan, 1997). In this context, it is pertinent to determine whether disturbance per se could increase levels of omnivory or generalism within populations. We observed relatively few shifts in diet related to treatments suggesting that this is not the case. On the contrary, we did observe increases in specialization in *P. decentis* in 2004. One possible explanation for this increased specialization could be related to increased populations of the large aspen tortrix (*Choristoneura conflictana* [Walker]) throughout the EMEND site and northwestern Alberta. *P. decentis* is a known climber of trees and predator of tree feeding caterpillars (Larochelle and Larivière, 2003) Between 2000 and 2003, relatively high levels of defoliation attributable to large aspen tortrix were reported for this region (Alberta Sustainable Resource Development 2000, 2001, 2002, 2003).

It is possible that *P. decentis* fed preferentially tortrix caterpillars still present following outbreaks during this period thus limiting the variability observed in isotopic N value. The same trend as been found in year related $\delta^{13}C$ variations of *P.adstrictus* and *S. haematopus*.

The lack of changes in SD of both $\delta^{13}C$ and $\delta^{15}N$ corroborate these assumptions and suggests that even in disturbed habitats, diet breadth is relatively constant in generalist predators. This implies that even thought some species are known to be generalists and/or omnivores they are nonetheless linked to particular types of resources in the landscape and they do not have the ability to change their prey types *ad libitum*.

1.5.4 Stable isotopes and the coarse filter approach

While stable isotopes can be a useful tool for describing feeding associations this approach is not without limits. For example, changes in resource use may not always be reflected in the isotopic signature of a consumer if these resources (or prey species) have similar isotopic signatures. Unfortunately, soil food webs are known to hold great functional redundancy (Moore *et al.*, 2004 ; Polis, 1991), which implies that many species may have similar isotopic signatures (Post, 2002). Furthermore, it is impossible, with stable isotopes, to detect the degree of generality at the level of the individual because SIV are an integrated mean of an individual's diet and do not provide information about the variance of that mean. Hence, generality and/or omnivory changes that might have occurred at the individual level would not have been detected.

One possible bias of our study is the choice of the species themselves; we chose species that were abundant throughout the experiment in order to estimate standard deviations in isotopic signatures (as a measure of omnivory and generalism). It is possible that these species rely on resources unaffected by harvest. Continued characterization of the SIV other species that were more adversely affected by harvest intensity is thus warranted.

1.6 Conclusion

Harvesting is known to affect many features within boreal forests including soil temperature and moisture, flows of energy and nutrients, density of dead roots and slash (Shaw *et al.*, 1991). Changes in these factors have been linked to changes in many organisms at the base of the food web including caterpillars (Summerville and Crist, 2002), mites (Lindo and Visser, 2004), collembola (Bird, Coulson and Fisher, 2004 ; Hannam, Quideau and Kishchuk, 2007) and bacteria (Hannam, Quideau and Kishchuk, 2007). Throughout our

study, isotopic signatures and presumably the net result of feeding behaviours were relatively unaffected by harvesting. Nonetheless, harvesting does alter abundances of numerous species at the EMEND site (Jacobs, Work and Spence, 2008), therefore, it is possible that our species simply cannot change their feeding behaviours after disturbance. By stipulating that species have evolved with natural disturbances, the coarse filter management approach suggests that the ability of species to adapt quickly to new disturbances is limited and thus suggests a need to maintain pertinent habitat elements following management activities. The fact that we found no clear evidence that generalist predators have the ability to drastically change their feeding behaviours following harvesting suggests that preservation of habitat structures, particularly those that maintain underlying carbon sources such as leaf litter and lower trophic level consumers such as detritivores and herbivores, may have significant benefits for maintaining abundance and diversity of higher level consumers.

1.7 Acknowledgement

We would like to thank Fangliang He, SFMN grant, Bruce Macnab (SFMN travel grant) for funding this research. Significant funding also was provided by Daishowa-Marubeni, Canadian Forest Products and Manning Diversified Forest Products. We would also like to thank Dave Shorthouse, Jason Edwards, Charlene Hahn, and other members of the EMEND core crew for their help with specimen collecting and logistics in the field. We also thank personal of the CEF (centre d'étude de la forêt), Jenna Jacobs, Simon Paradis, Dave Gervais and Annie Hibbert for help with writing and development of ideas.

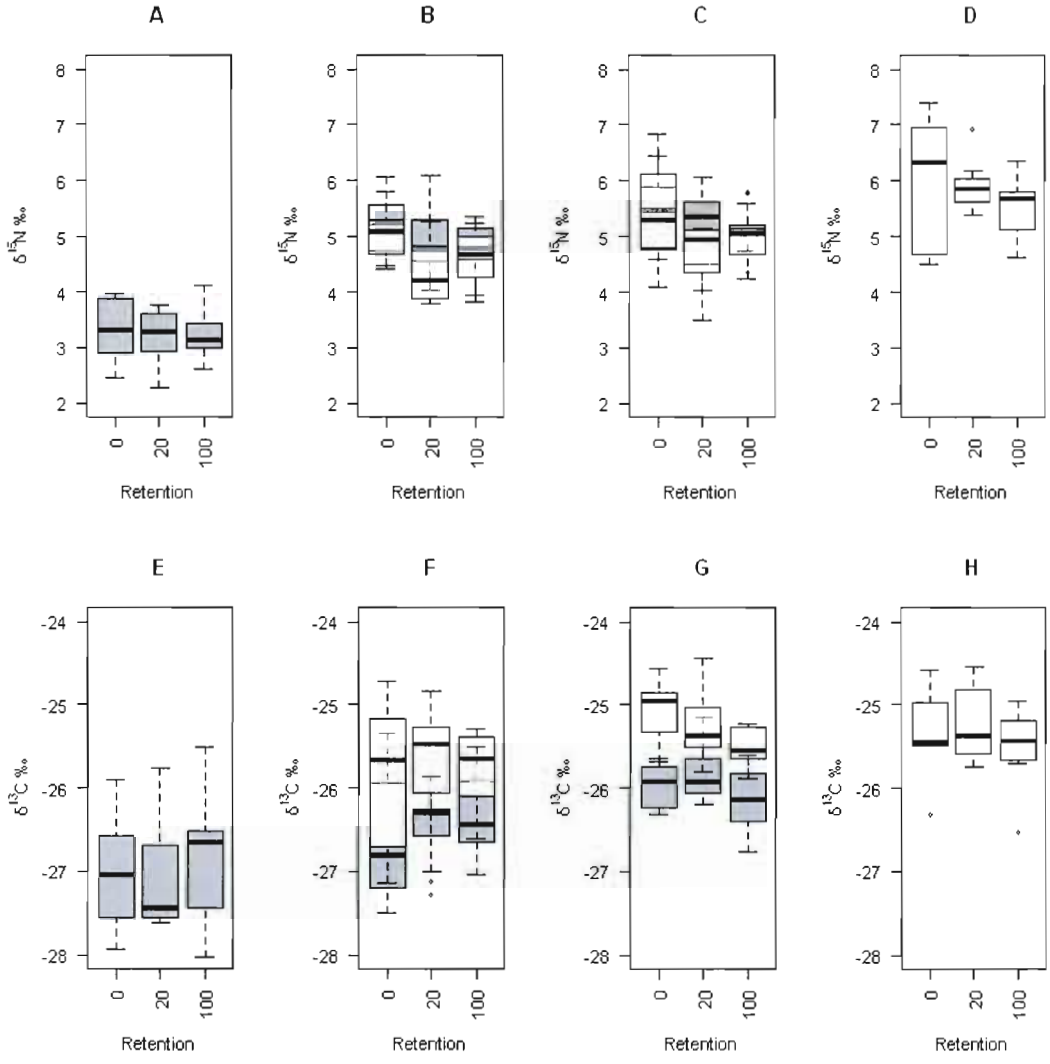

Figure 1.1. Boxplots of $\delta^{15}N$ and $\delta^{13}C$ values for *P. decentis* (A, E), *P. adstrictus* (B, F), *S. pleuralis* (C, G), and *S. haematopus* (D, H) respectively plotted by retention level and cover type. White bars correspond to stable isotope values observed in deciduous stands while gray bars correspond to conifer dominated stands. Note that light gray areas are created when the white and gray bars overlap. Dark bars correspond to median observations, boxes correspond to 25% and 75% quantiles and whiskers correspond to 95% confidence intervals.

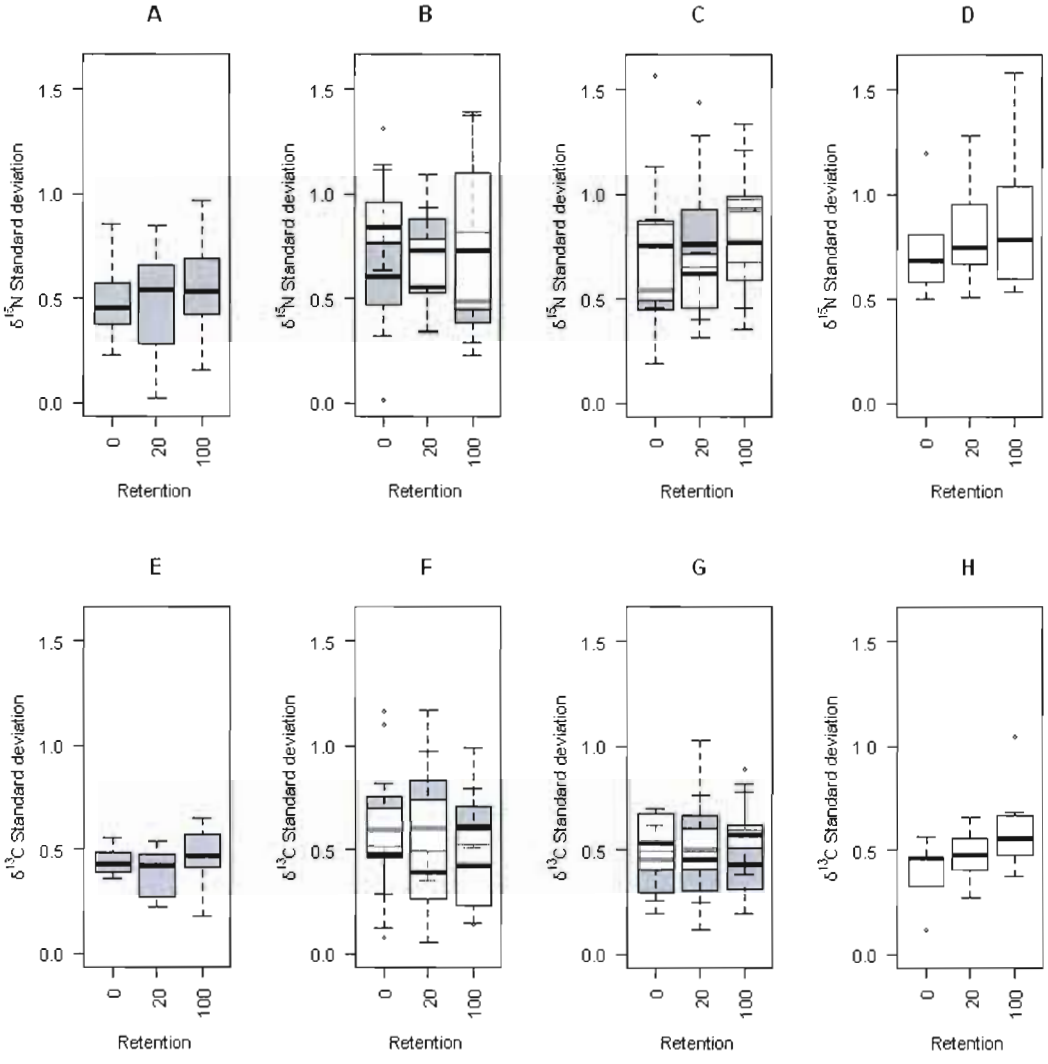

Figure 1.2. Boxplots of $\delta^{15}N$ and $\delta^{13}C$ standard deviation values for *P. decentis* (A, E), *P. adstrictus* (B, F), *S. pleuralis* (C, G), and *S. haematopus* (D, H) respectively plotted by retention level and cover type. White bars correspond to stable isotope standard deviation values observed in deciduous stands while gray bars correspond to conifer dominated stands. Note that light gray areas are created when the white and gray bars overlap. Dark bars correspond to median observations, boxes correspond to 25% and 75% quantiles and whiskers correspond to 95% confidence intervals.

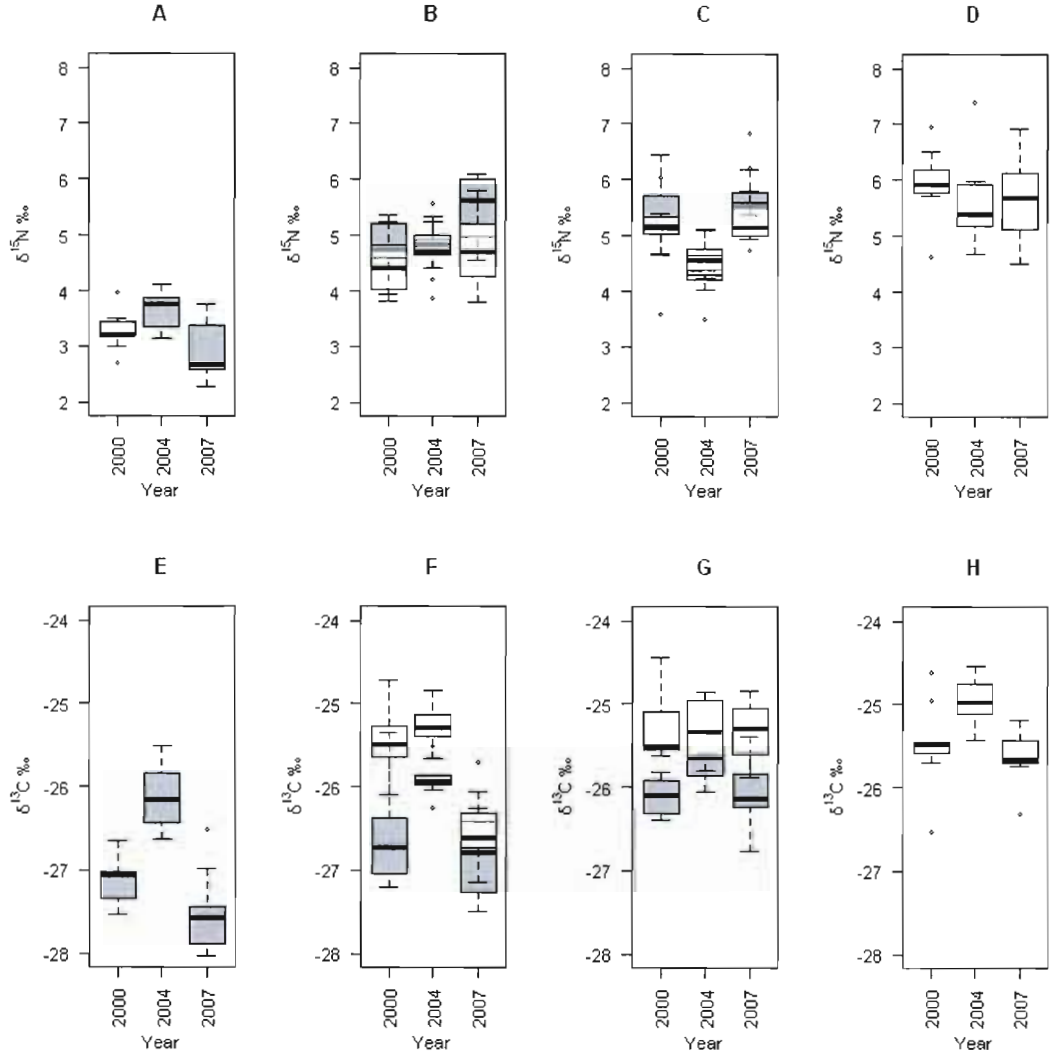

Figure 1.3. Boxplots of $\delta^{15}N$ and $\delta^{13}C$ values for *P. decentis* (A, E), *P. adstrictus* (B, F), *S. pleuralis* (C, G), and *S. haematopus* (D, H) respectively plotted by year and cover type. White bars correspond to stable isotope values observed in deciduous stands while gray bars correspond to conifer dominated stands. Note that light gray areas are created when the white and gray bars overlap. Dark bars correspond to median observations, boxes correspond to 25% and 75% quantiles and whiskers correspond to 95% confidence intervals. In these plots, stable isotope values have been pooled by retention treatment and all boxes based on n=9.

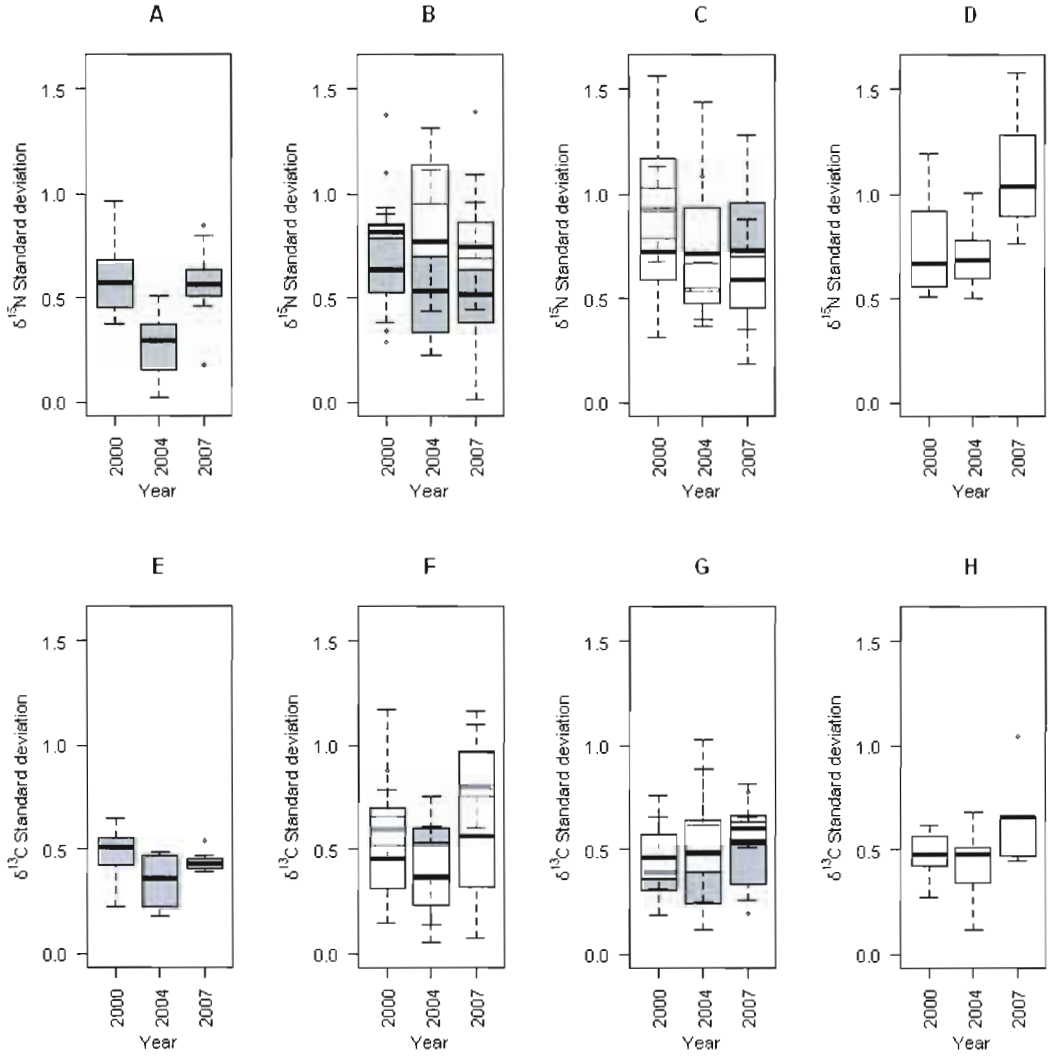

Figure 1.4. Boxplots of $\delta^{15}N$ and $\delta^{13}C$ standard deviation values for *P. decentis* (A, E), *P. adstrictus* (B, F), *S. pleuralis* (C, G), and *S. haematopus* (D, H) respectively plotted by year and cover type. White bars correspond to stable isotope standard deviation values observed in deciduous stands while gray bars correspond to conifer dominated stands. Note that light gray areas are created when the white and gray bars overlap. Dark bars correspond to median observations, boxes correspond to 25% and 75% quantiles and whiskers correspond to 95% confidence intervals. In these plots, stable isotope values have been pooled by retention treatment and all boxes based on n=9.

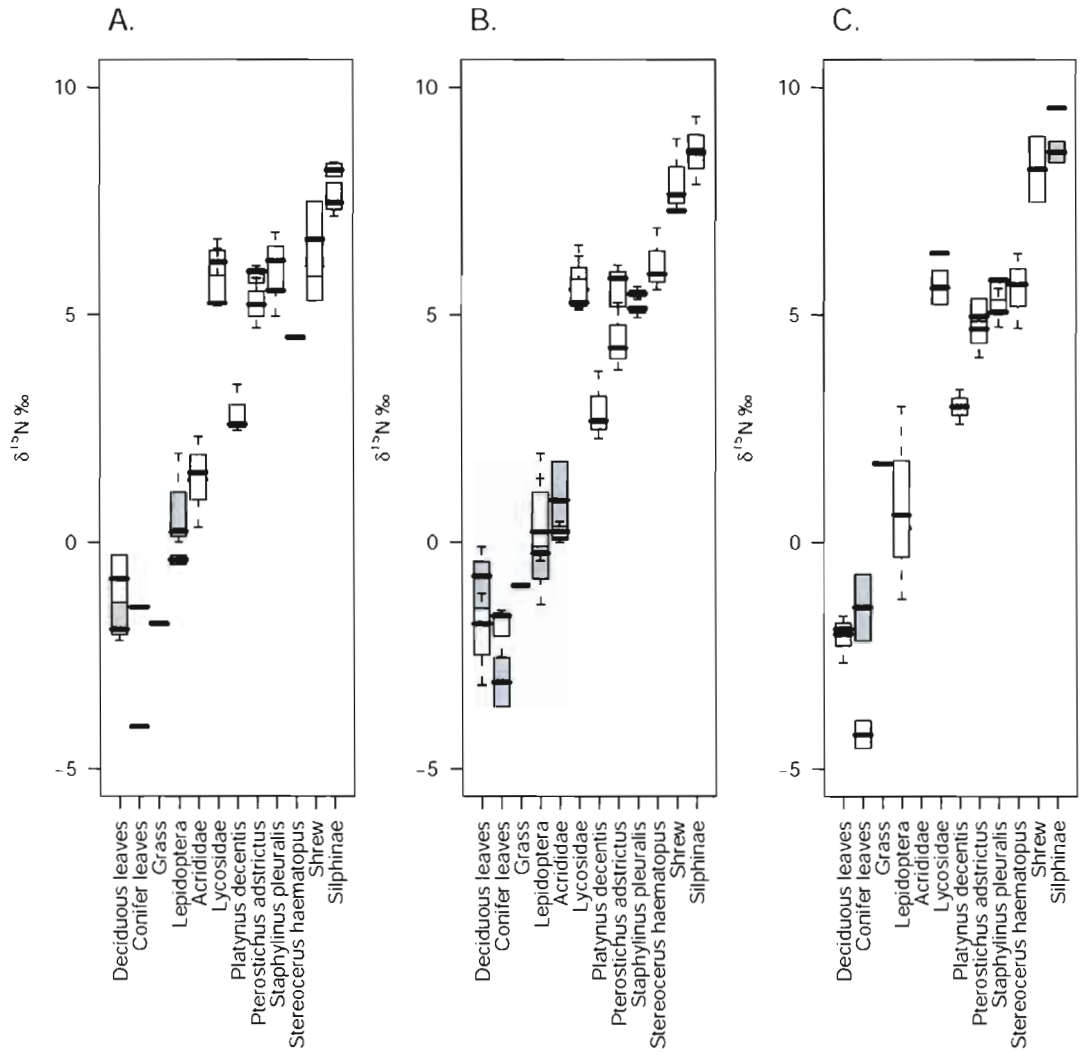

Figure 1.5. Boxplots by A. Clearcut, B. 20% retention and C. Uncut stands. From 2007. White bars correspond to stable isotope standard deviation values observed in deciduous stands while gray bars correspond to conifer dominated stands. Dark bars correspond to median observations, boxes correspond to 25% and 75% quantiles and whiskers correspond to 95% confidence intervals.

.

Table 1.1: Species mean $\delta^{13}C$ and $\delta^{15}N$ with standard deviations by years, cover type and treatment.

	0						20						100					
	2000		2004		2007		2000		2004		2007		2000		2004		2007	
	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
CDOM $\delta^{13}C$																		
Pterostichus adstrictus	-25.300	0.628	-25.384	0.110	-25.741	0.314	-25.326	0.292	-25.063	0.350	-25.330	0.048	-26.854	0.253	-26.455	0.485	-26.266	0.488
Staphylinus pleuralis	-25.071	0.497	-25.154	0.614	-25.464	0.202	-24.859	0.008	-25.403	0.381	-25.520	0.218	-25.195	0.440	-25.302	0.285	-25.551	0.310
Stereocereus haematopus	-25.462	0.018	-25.257	0.553	-25.731	0.793	-24.775	0.277	-24.778	0.331	-25.192	0.242	-26.320	na	-25.496	0.279	-25.548	0.206
DDOM $\delta^{13}C$																		
Platynus decentis	-27.104	0.117	-26.022	0.175	-27.594	0.532	-27.293	0.256	-26.066	0.424	-27.575	0.043	-26.994	0.458	-26.214	0.612	-27.318	0.763
Pterostichus adstrictus	-26.451	0.973	-26.684	0.393	-26.701	0.354	-25.930	0.054	-26.042	0.195	-25.772	0.244	-27.249	0.237	-26.607	0.582	-26.534	0.021
Staphylinus pleuralis	-26.152	0.211	-26.008	0.089	-26.181	0.313	-25.648	na	-25.617	0.459	-25.771	0.198	-25.642	0.709	-25.834	0.412	-26.436	0.320
CDOM $\delta^{15}N$																		
Pterostichus adstrictus	4.716	0.351	4.230	0.533	4.441	0.722	5.103	0.357	4.338	0.538	4.798	0.168	5.247	0.552	4.450	0.753	4.590	0.482
Staphylinus pleuralis	5.538	0.447	4.418	0.741	5.182	0.135	4.609	0.021	4.332	0.803	4.484	0.217	5.997	0.943	5.078	0.120	5.218	0.320
Stereocereus haematopus	6.536	0.413	5.931	0.236	5.400	0.667	6.029	1.920	5.608	0.329	5.445	0.461	4.509	na	6.130	0.706	5.578	0.834
DDOM $\delta^{15}N$																		
Platynus decentis	3.456	0.117	3.369	0.256	3.051	0.458	3.880	0.175	3.485	0.424	3.586	0.612	2.839	0.532	2.913	0.043	2.987	0.763
Pterostichus adstrictus	4.851	0.304	4.698	0.637	4.626	0.705	5.103	0.562	4.650	0.232	4.852	0.068	5.826	0.337	5.485	0.824	4.966	0.555
Staphylinus pleuralis	5.324	0.977	5.652	0.455	5.155	0.060	4.101	na	4.276	0.238	4.821	0.401	5.746	0.408	5.483	0.140	5.439	0.610

Table 1.2: ANOVA table indicating the significance of factors in the linear mixed models for each specie and response variable

	δ^{13}C Means				δ^{15}N Means				δ^{13}C Sandard deviations				δ^{15} N Standard deviations			
	numDF	denDF	F-value	p-value	numDF	denDF	F-value	p-value	numDF	denDF	F-value	p-value	numDF	denDF	F-value	p-value
Pterostichus adstrictus																
Cover	1	12	31.96	**0.0001**	1	12	5.96	**0.0311**	1	12	2.53	0.1380	1	12	3.09	0.1045
Treatment	2	12	0.59	0.5691	2	12	4.81	**0.0293**	2	12	0.35	0.7086	2	12	0.27	0.7712
Time since harvest (TSH)	2	23	34.96	< **0.0001**	2	23	4.20	**0.0279**	2	20	5.41	**0.0132**	2	20	0.26	0.7752
Treatment xTSH	4	23	2.25	0.0951	4	23	0.60	0.6656	4	20	0.39	0.8112	4	20	1.36	0.2827
Cover x Treatment	2	12	0.28	0.7584	2	12	0.83	0.4600	2	12	0.05	0.9475	2	12	1.03	0.3865
Cover x TSH	2	23	5.27	**0.0130**	2	23	1.29	0.2939	2	20	0.41	0.6681	2	20	0.49	0.6190
Cover x Treatment x TSH	4	23	0.34	0.8462	4	23	0.06	0.9917	4	20	1.02	0.4207	4	20	0.52	0.7242
Staphylinus pleuralis																
Cover	1	12	27.68	**0.0002**	1	12	1.29	0.2786	1	12	0.94	0.3510	1	12	0.11	0.7436
Treatment	2	12	3.07	0.0840	2	12	3.55	0.0616	2	12	0.31	0.7380	2	12	0.48	0.6305
Time since harvest (TSH)	2	21	1.59	0.2266	2	21	18.76	< **0.0001**	2	21	1.04	0.3706	2	21	2.79	0.0841
Treatment xTSH	4	21	0.64	0.6383	4	21	0.71	0.5934	4	21	1.02	0.4202	4	21	1.13	0.3708
Cover x Treatment	2	12	0.31	0.7378	2	12	1.61	0.2398	2	12	0.36	0.7026	2	12	0.86	0.4493
Cover x TSH	2	21	2.32	0.1234	2	21	0.71	0.5009	2	21	0.05	0.9490	2	21	1.34	0.2839
Cover x Treatment x TSH	4	21	0.80	0.5417	4	21	1.38	0.2761	4	21	0.60	0.6697	4	21	0.91	0.4762
Platynus decentis																
Treatment	2	6	0.69	0.5377	2	6	0.10	0.9075	2	6	1.08	0.3975	2	6	0.26	0.7784
Time since harvest (TSH)	2	10	18.65	**0.0004**	2	10	7.68	**0.0095**	2	9	2.93	0.1046	2	9	5.23	**0.0311**
Treatment x TSH	4	10	0.29	0.8795	4	10	0.52	0.7263	4	9	0.68	0.6229	4	9	0.07	0.9885
Sterocereus haematopus																
Treatment	2	6	0.44	0.6660	2	6	1.84	0.2374	2	6	0.97	0.4310	2	6	0.18	0.8436
Time since harvest (TSH)	2	8	8.08	**0.0120**	1	4	0.42	0.5512	1	3	34.04	**0.0100**	1	3	0.07	0.8095
Treatment xTSH	4	8	1.75	0.2321	2	4	0.21	0.8184	2	3	42.63	**0.0063**	2	3	2.09	0.2699

1.8 References

In order to cut back paper use we provide references for this article at the end of this document along with all other cited references in the thesis.

CHAPITRE II

THE EFFECTS OF SIZE ON THE TROPHIC LEVEL OF BOREAL MIXEDWOOD BEETLES

Félix Longpré and Timothy T. Work

Félix Longpré was responsible for the planning, field work, identification of specimens, compiling of data and analysis. Timothy T. Work contributed as director throughout all stages and co-author of the article. Funding was provided in part by a SFMN grant awarded to Fangliang He (University of Alberta). This article will be submited to Oecologia after corrections.

2.1 Abstract

Among other life history traits, body size determines in part overall metabolic costs to organisms, the size of potential prey and predators and is broadly considered an important factor affecting food web structures and species trophic interactions. For organisms within a feeding guild which by definition share similar resources, body size may also become an important factor determining competitive superiority. In ecological studies, nitrogen isotopic values ($\delta^{15}N$) are used to determine the trophic position of organisms and carbon isotopic values ($\delta^{13}C$) are used to identify major differences in carbon sources at the base of a food chain. We tested whether body length increases trophic position (defined as $\delta^{15}N$) for 35 abundant species of Coleoptera within herbivore, fungivore and predator guilds in the boreal mixedwood forest. All arthropods for this study were collected from uncut stands in the Ecosystem Disturbance Management Emulating Natural Disturbance (EMEND). We observed a significant negative linear relationship between body size and mean trophic position of individual species in the fungivore guild (R^2= 0.535, p= 0.025) and no significant relationship between body size and mean trophic position in herbivores and predators. As expected, all species found in both cover types exhibited higher mean $\delta^{13}C$ in conifer dominated stands compared to deciduous dominated stands. If species do not adjust their feeding behavior according to cover type, we have to consider the possibility that compensatory effects and short time adaptation following a major perturbation will unlikely be the result of feeding behavior modifications.

2.2 Introduction

Even though classic food-web models like the cascade model and the niche model provide good description of food-web structures; they lack concrete mechanisms explaining these structures (Locuille and Loreau, 2005). Therein, recent approaches linking food web structure to community ecology and ecosystem functions favor the use of evolutionary and trait related mechanisms to create new models (Caldarelli, Higgs and McKane, 1998 ; Drossel, Higgs and McKane, 2001 ; Loeuille and Loreau, 2005). Since competition and prey-predator relationships are key elements in the understanding of food web structures and species coexistence (Drossel, Higgs and McKane, 2001), it is also important to understand the role of traits such as body size in modeling food web structure and evolution (Loeuille and Loreau, 2005).

Among other life history traits, body size determines in part overall metabolic costs to organisms, the size of potential prey and predators and is broadly considered an important factor affecting food web structures and species trophic interactions (Cohen *et al.*, 1993 ; Memmott, Martinez and Cohen, 2000 ; Warren and Lawton, 1987). In the particular case of size structured food-webs, small species are most often consumed by bigger ones and trophic position typically increases with body size (Cohen *et al.*, 1993). In very speciose ecosystems, food web studies traditionally use species aggregated into guilds that reflect their functional and diet similarities (i.e. herbivores, fungivores, predators) (Cohen, 1989 ; Menge and Sutherland, 1987). For organisms within a feeding guild which by definition share resources, body size may also become an important factor determining competitive superiority. Predation and competition become inexorably linked as intraguild predation: whereby an intraguild predator consumes a competing species in lieu of a shared prey species (Polis, Myers and Holt, 1989). Intraguild predation is frequent amongst terrestrial arthropods (Mabelis, 1984 ; Polis and McCormick, 1987 ; Reichert and Cady, 1983 ; Robinson, 1987). If body size plays an important role in structuring communities through trophic and competitive interactions, distribution of body sizes among species and any relation to trophic interactions could be considered a relevant functional trait that is pertinent in defining patterns of diversity.

Conservation of biodiversity continues to be an important concern particularly in managed forest ecosystems. Ground beetles, rove beetles and saproxylic beetles are becoming some of the better studied groups of animals in biodiversity studies evaluating the effects of forest management (Jacobs, Spence and Langor, 2007 ; Jacobs, Work and Spence, 2008 ; Langor and Spence, 2006 ; Work *et al.*, 2008). In this context, assemblages of these insect groups are used to test whether different management strategies effectively emulate natural disturbances as prescribed in the coarse filter approach to conservation (Armstrong *et al.*, 2003 ; Attiwill, 1994 ; Bergeron and Harvey, 1997 ; Lindenmayer, 1999 ; McLaren, Thompson and Baker, 1998 ; Noss, 1999 ; Spence, 2001). This approach is based on the principle that there are long-term associations and adaptations of organisms to natural disturbances and that conservation of habitats should be an efficient way to maintain most species when it is impractical to account for each species individually (Attiwill, 1994 ; Hunter, Jacobson and Webb, 1988). As forest harvesting is known to alter plant composition and faunal biodiversity and perhaps the functional traits related to distribution of body sizes at least initially (Drapeau *et al.*, 2003 ; Heliola, Koivula and Niemela, 2001 ; Koivula, Kukkonen and Niemelä, 2002); it may also alter resources, food webs and trophic interactions.

Direct observation of feeding behaviors in terrestrial arthropods is very limited as these interactions involve a large number of cryptic organisms in often inaccessible habitats (Polis, 1991). Therefore, characterization of arthropod food webs, resource use and feeding strategies are facilitated by the use of stable isotopes as the stable isotope values for elements like carbon and nitrogen within an organism reflect those of its diet (Halaj, Peck and Niwa, 2005 ; Peterson and Fry, 1987 ; Post, 2002). These techniques have been used extensively in the study of arthropod food webs (Halaj, Peck and Niwa, 2005 ; McNabb, Halaj and Wise, 2001 ; Ponsard and Amlou, 1999) and soil communities (Scheu and Falca, 2000 ; Scheu and Folger, 2004). They also have been used to study arthropod food webs in uncut forests, by the characterization of general trophic groups like predators and detritivores (Ponsard and Arditi, 2000 ; Scheu and Falca, 2000).

The term fractionation (Δ) is used to describe differences in stable isotope values between a consumer and its food source (Post, 2002). Nitrogen and carbon fractionation values for one

trophic level are 3.4 ± 1.1‰ and 0.4 ± 1.4‰ respectively (DeNiro and Epstein, 1978, 1981 ; Minagawa and Eitaro, 1984). Because nitrogen isotopic values ($\delta^{15}N$) increase or fractionate appreciably with each trophic level they are often used to determine the trophic position of organisms (Post, 2002). Carbon isotopic values ($\delta^{13}C$) are comparably less sensitive to changes in trophic levels and are used to identify major differences in carbon sources at the base of a food chain (Post, 2002).

Here, we tested whether body length is correlated with trophic position (defined as $\delta^{15}N$) for 35 abundant species of Coleoptera from herbivore, fungivore and predator guilds in the boreal mixedwood forest. We initially hypothesized that increased body size would be correlated with trophic position for predators due to the combined effects of competition and predation inherent to any intra-guild predation interactions that may exist in this system. It has been suggested elsewhere that IGP interactions are abundant among forest arthropods (Ponsard and Arditi, 2000). We expected body size to have less of an effect on trophic position within herbivore and fungivore guilds, as these effects would be mediated primarily by competition alone and these groups are likely limited by predators rather than lack of resources.

2.3 Methodology

2.3.1 Study site

We collected all arthropods for this study from uncut stands in the Ecosystem Disturbance Management Emulating Natural Disturbance (EMEND) experimental site in the Lower Foothills ecoregion of Alberta, Canada north west of Dixonville (56°46'13''N, 118°22'28''W). The site rests between 667 and 880 meters and covers an area of 24 Km^2 (Work *et al.*, 2004). EMEND soils are relatively rich with a fine textured lacustran (Kishchuk, 2004). The site is characteristic of western boreal mixed forest and is dominated by *Populus tremuloides* Michaux (trembling aspen), *Populus balsamifera* L. (balsam poplar), *Picea glauca* (Moench) Voss (white spruce), *Picea marianna* Miller (black spruce) and *Abies balsamea* (Linné) Miller (balsam fir). We used two dominant cover types: the deciduous dominated stands (DDOM), which were composed of >70% *P. tremuloides* and *P. balsamifera* and the conifer dominated stands (CDOM), composed of >70% *P. glauca* and *P.*

marianna. The DDOM and CDOM cover types respectively represent the early and later stages of stand development common in generalized views of boreal forest succession in this area (Lieffers *et al.*, 1996).

2.3.2 Arthropod sampling

Specimens were obtained from past pitfall trap collections (Work *et al.*, 2004) and flight intercept trap collections (Jacobs, Spence and Langor, 2007) used in previously published studies. The beetles were collected in 2000 and 2004 and were stored in 70% ethanol for preservation. The effects of preservation on isotopic values of other arthropods are negligible (Ponsard and Amlou, 1999 ; Sarakinos, Johnson and Vander Zanden, 2002) and since all our samples were preserved in the same manner, we consider any biases related to preservative to be uniform for all specimens. We targeted 35 abundant beetle species from three different guilds: 10 species of herbivores (primarily xylophagous and phloeophagous species), 9 species of fungivores and 16 species of predators. All specimens used in this study were identified to species using a dissecting microscope and taxonomic keys developed by C. Lindroth and others (Ball and Nègre, 1972 ; Bousquet, 1990 ; Bright, 1976 ; Brooks, 1960 ; Cambell, 1973 ; Cambell, 1982 ; Fall, 1899; Fall, 1933 ; Hoebeke, 1992 ; Kasantsev, 1992 ; Leschen, 1996 ; Lindroth, 1966 ; Smetana, 1971 ; Younga-Endrody, 1981)

2.3.3 Stable isotope content

We rinsed specimens with distilled water then freeze dried them in a LabconcoTM Freeze dry system Freezone 12 lyophiliser. Heavy insects (>0.8 micrograms) were ground with a mortar and pestle before subsamples of 0.6 to 0.8 micrograms were encapsulated in tin cups while lighter insects (<0.8 micrograms) were encapsulated in tin cups without prior grounding. We measure carbon and nitrogen isotopic ratios using a Micromass (GVI) Isoprime mass spectrometer. $\delta^{13}C$ and $\delta^{15}N$ values are expressed in per mil (‰) and are calculated with the following formula: $\delta E = [(R_{sample} / R_{standard} - 1)] * 1000$. E is the element and R is the ratio of heavy to light isotope ($R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$) of the sample and the standard material. The standard material for carbon is PeeDee limestone and air for nitrogen (Peterson and Fry, 1987). Raw data was corrected with a calibration curve based on two

reference materials: leucine ($\delta^{13}C$=-28,50‰; $\delta^{15}N$=-0,26‰) and DORM-2 ($\delta^{13}C$=-17,35‰; $\delta^{15}N$=+14,36‰)

2.3.4 Data analysis

We measured the carbon and nitrogen isotopic values of 549 insect specimens: 160 herbivores, 63 fungivores and 326 predators. Here, the term herbivore encompasses all species that feed on plant material. Finer feeding differences within this group will be addressed further below. For each guild, we tested the relation between length and $\delta^{15}N$ with linear regression. Here, we used species as analytical replicates because we did not have size measurements for individuals; rather we used mean size reported for given species.

When species were found in both cover types, we tested the influence of cover type on species $\delta^{13}C$ and $\delta^{15}N$ with a series of One-way ANOVA. One-way ANOVA tests where also used to investigate $\delta^{15}N$ differences between guilds and $\delta^{15}N$ differences between species within guilds; we then used Tukey HSD *post hoc* tests to examine all pairwise comparisons. We acknowledge that taxa could have been divided into finer feeding categories (i.e. sap feeders, foliage feeders and xylophagous species for the herbivore guilds), but a lack of individuals prevented us from analyzing finer feeding categories statistically. Nevertheless, we compared isotopic signatures graphically to further elucidate the variability in feeding modes within our main guilds. All statistical tests and figures were done using R 2.7.0 (R Development Core Team 2007).

2.4 Results

Because species vary in habitat associations, we were unable to compare differences in isotopic C and N between deciduous and coniferous cover types for all species. With the exception of *Dichelotarsus piniphilus* (Eschscholtz), all species found in both cover types exhibited higher mean $\delta^{13}C$ in conifer dominated stands compared to deciduous dominated stands (Table 2.1 and Figure 2.1), these differences were statistically significant for 6 of the 14 species (1 herbivore, 2 fungivores and 5 predators). These species include *Epuraea linearis* Mäklin, *Rhizophagus brunneus* Horn, *Pterostichus adstrictus* Eschscholtz, *Quedius velox* Smetana, *Quedius rusticus* Smetana, *Staphylinus pleuralis* LeConte (Table 2.1).

Species $\delta^{15}N$ was generally not affected by cover type with the exception of *Ctenicera nitidula* LeConte ($t = -4.707_{9.43}$, p-value = 0.0010) and *Q. rusticus* ($t = -2.120_{24.2}$, p-value = 0.0445) (Table 2.1 and Figure 2.2).

As expected, significant $\delta^{15}N$ differences were found between each guild ($F_{2, 534} = 56.84$, $p < 0.0001$) (Table 2.2 and Figure 2.2). Predators yielded the highest $\delta^{15}N$ values (4.67‰), followed by fungivores (2.74‰) and herbivores (-0.77‰).

We also observed significant $\delta^{15}N$ differences between individual species within the herbivore ($F_{11, 165} = 13.85$, $p < 0.0001$), fungivore ($F_{6, 39} = 3.62$, $p = 0.0059$) and predator ($F_{14, 299} = 19.70$, $p < 0.0001$) guilds (Table 2.2). 2.3 presents $\delta^{15}N$ means and means comparisons for all species pairs using Tukey-Kramer HSD test. We observe clear $\delta^{15}N$ distinctions between species occupying the lowest and highest trophic positions of each guild. Nonetheless, we observe considerable $\delta^{15}N$ overlap between species within all guilds (Table 2.3 and Figure 2.2).

We observed a significant negative linear relationship between body size and mean trophic position of individual species in the fungivore guild ($R^2 = 0.535$, $p = 0.025$) and no significant relationship between body size and mean trophic position in herbivores and predators (Table 2.4 and Figure 2.3). Among the three feeding groups, predators have the largest range of size classes and are generally larger than fungivores and herbivores which had smaller ranges of size (Figure 2.3).

2.5 Discussion

2.5.1 Body size and trophic position

Initially we expected size to be an important functional trait for predators who participate in IGP relationships. Overall we found little evidence to support that larger body size increased trophic position for a relatively large assemblage of boreal arthropods, even when analyzed as separate feeding guilds. In fact, the only significant size/trophic height relation observed was that of fungivores and was negative. We acknowledge that size structured food webs are present in many ecosystems, nonetheless, the lack of positive relation between body size and $\delta^{15}N$ in our study suggests that other factors may be important in the determination of food web structure.

For instance, predator size might be influenced by the nature of resources at the base of the food web. Because detritus is thought support longer trophic chains than do live primary producers (Hairston, 1993) and given that detritus-feeding animals are often very small when compared to herbivores it is probable that predator will be smaller in detritus based food webs compared to live vegetation based food webs. Furthermore, it is probable size vs. trophic height relations manifest more in specific subcompartments of food webs rather than at the whole food web level. For example, a fungus sporocarp can attract particular fungivores and predators that are rarely found elsewhere in the ecosystem. This implies that even though predators probably feed on organisms that are smaller then them (Cohen *et al.*, 1993), size cannot explain the organization of entire food webs when those encompass numerous energy pathways in different types of habitat. For example, in our study, the three predators with the highest $\delta^{15}N$ were relatively small staphylinids. In boreal mixedwoods, many staphylinids, particular in the genus *Tachinus* and numerous Alleocharineae species are associated with mushrooms where they may be feeding on fungivorous diptera (Hammond and Lawrence 1989); in this case, smaller body sizes could allow the exploitation of resources limited to small habitats. By feeding on fungal consumers, these smaller species may actually be tertiary or higher-level consumers. This contrasts with the situation of *Platynus decentis* (Say): a predator that exhibited low $\delta^{15}N$ values. This relatively big carabid beetle is known to prey on Lepidoptera larvae (Larochelle and Larivière, 2003) and is probably too big to get inside mushroom carpophores. In this way, even though these two different predators are a part of the whole food web of forest organisms, size vs. trophic height relations should probably be analyzed for the grazing and the detritus pathways separately as body size could primarily determine habitat niches rather than trophic positions across the whole food web.

Other factors could explain the absence of positive relationships between body size and $\delta^{15}N$. In his 1991 critique of food web theory, Polis underlined the importance of factors other than size such as age structured predation. In this scenario, mature individuals of one species prey on the juveniles of a second species but may later face reciprocal or 'reprisal' predations from adults of the second species (Polis, 1991). Such detailed mechanisms cannot be readily verified using the approach we used here but could be resolved through more detailed species-level studies. Furthermore, even though Loeuille and Loreau stated that size

and trophic position are closely associated in their food web evolution model, they also showed that high levels of generalism and omnivory tend to create less organized trophic structures, which translate into species being spaced homogeneously along a continuum of trophic positions (Loeuille and Loreau, 2005). Our results show similar trends, in the fact that most our predators are generalist omnivores with considerable consumption niche width and that we have observed substantial $\delta^{15}N$ overlap between the species within each guild. This suggests that we are witnessing the effect described by Loeuille and Loreau.

In addition, it is also possible that our sampling methods influenced the range of body sizes of our guilds. Pitfall traps are good at catching larger organisms (Work *et al.*, 2004) and intercept traps likely sample smaller, more vagile organisms that fly. The fact that predators had a large range of body sizes compared to the fungivores and herbivores (Figure 2.3) could be explained by the fact that our predators where collected from pitfall traps and intercept traps while fungivores and herbivores were collected solely from intercept traps.

The negative relationship we found between size and trophic position in fungivores was unexpected. This relationship appears to be driven by two species (*Trypodendron retusum* (LeConte) and *Trypodendron lineatum* (Olivier): subfamily Scolytidae) as the relationship becomes non-significant when they are removed. We classified *T. retusum* and *T. lineatum* as fungivores because unlike most scolytids which feed on wood and phloem, they are ambrosia beetles whose larvae feed on fungi. This fungi is provided by females which inoculate their galleries prior to depositing eggs (Bright, 1976). Since fungi typically have higher $\delta^{15}N$ then the plant material they consume (Trudell, Rygiewicz and Edmonds, 2004), we expected *T. retusum* and *T. lineatum* to be have considerably higher $\delta^{15}N$ than other Scolytidae in our study (*Dendroctonus ruffipennis* Kirby, *Dryocoetes affaber* Mannerheim, *Polygraphus rufipennis* Kirby, *Scierus annectans* LeConte, *Scierus pubescens* (Swaine) and *Xylechinus montanus* Blackman); surprisingly, this was not the case. The nitrogen signature of *T. retusum* and *T. lineatum* were very similar to the remaining xylophagous Scolytidae. This suggests that for ambrosia beetles a large proportion of the diet comes from woody tissues at least in the adult stage.

2.5.2 Cover type effects

When comparing cover-types, species in deciduous stands generally had lower $\delta^{13}C$ than those found in conifer stands. Conifer trees generally yield higher $\delta^{13}C$ values than deciduous trees with the conifer trees having a $\delta^{13}C$ about 1.5‰ higher than the deciduous trees (Brooks *et al.*, 1997 ; Takahashi and Miyajima, 2008). Dominant tree species are likely the most important source of carbon in the ecosystem and thus this effect is expected. Nonetheless, it is interesting to see that such differences persist in higher trophic levels and may suggest to a certain degree, a lack of mobility in these species.

The fact that we found very little significant differences in $\delta^{15}N$ in relation to cover type implies that species maintain their relative trophic position at both ends of the successional gradient of the boreal mixedwood. Studies have shown that cover type differences are important in the determination of insect assemblages (Jacobs, Work and Spence, 2008 ; Work *et al.*, 2004). Nonetheless, some species do occur in all cover types and we have to consider that for these species compensatory effects and short time adaptation following a major disturbance will unlikely be the result of feeding behavior modifications.

The differences in mean $\delta^{15}N$ between herbivores and other guilds are not wholly unexpected and concur with many previous studies (Bennett and Hobson, 2009 ; McNabb, Halaj and Wise, 2001 ; Ponsard and Arditi, 2000). Interestingly, we observed significant species level differences in $\delta^{15}N$ within guilds. This can be explained in part by the fact that the guilds we used were not defined at very fine levels of feeding categories since a lack of individuals prevented us from analyzing finer feeding categories statistically. This underscores the well demonstrated notion that broad feeding guilds, such as those prescribed at the family level may be insufficient for a detailed depiction of trophic relationships.

2.5.3 Species level differences

In many cases, species isotopic values could be explained with previously reported life history traits. The diverse $\delta^{15}N$ values found in fungivores may be explained in part by the fact that isotopic values are highly variable between fungi species (Trudell, Rygiewicz and Edmonds, 2004). This also suggests fungivores could specialize on different fungi.

In the predators, the 4 lowest $\delta^{15}N$ values were observed in *Rhizophagous. brunneus*, *Dichelotarsus piniphilus*, *Platynus decentis* (Say) and *Cucujus Clavipes* Fabricius. *Rhizophagous. brunneus* is a known predator of scolytids (Arnett and Thomas, 2001a). The approximate 3.4 ‰ $\delta^{15}N$ difference observed between *Rhizophagous brunneus* and the scolytids indicates a clear trophic step and provides additional evidence of its specialization on bark beetles. The case of *Platynus decentis* is somewhat similar to that of *Rhizophagous brunneus*, as the former has also been reported to feed on herbivores, in particular on lepidopteran larvae (Larochelle and Larivière, 2003). *Dichelotarsus piniphilus* is in the Cantharidae family which are often found on flowering plants and are known to prey on other insects as well as feed on nectar and pollen (Arnett and Thomas, 2001b). A diet composed of both insects and plant material could explain the low $\delta^{15}N$ that we have observed. *Cucujus clavipes* is a known generalist predator of insect larvae under the bark of dead trees (Arnett and Thomas, 2001b). We did not measure the possible prey of this species, but since the $\delta^{15}N$ values of *Cucujus clavipes* are similar to those of *Rhizophagous brunneus*, we put forward that it probably consumes prey feeding on cambium similar in isotopic signature to the scolityds.

2.6 Conclusion

We recognize that size trophic webs occur in many ecosytems. Nonetheless, our results demonstrated no size structured food web in the boreal mixedwood Coleoptera that we sampled. We also found that cover types did not impact the trophic level species, which suggests that major trophic shifts are not occurring along the succession processes and that compensatory response subsequent to disturbance are unlikely linked to dietary changes. This provides additional support on the importance of species conservation to preserve redundancy in functional traits. Different pools of energy (i.e. fresh or dead matter) are found at the based of boreal forest arthropods food webs and from them emerges different trophic pathways. It is probable that size plays and important role in determining the niche of species and the trophic pathways they take part in.

To our knowledge, this article provides the first species level characterization of isotopic nitrogen and carbon values of common ground beetles, rove beetles and saproxylic beetles of the boreal mixedwood in Canada. Furthermore, we provided more evidence in accord with

several previously recognized feeding habits of concerned species as well as some new interrogations on feeding habits of others. An interesting venue for future isotopes research would be to investigate isotopic differences between the food webs base on detritus (brown food web) and fresh vegetation (green food web) as here, it is likely that we have sampled predators that originate from both the grazing and the detritus pathways at the precise point where the "brown" and "green" worlds meet.

2.7 Acknoledgements

We would like to thank Fangliang He, SFMN grant, Bruce Macnab (SFMN travel grant) for funding this research. Significant funding also was provided by Daishowa-Marubeni, Canadian Forest Products and Manning Diversified Forest Products. We would also like to thank Dave Shorthouse, Jason Edwards, Charlene Hahn, and other members of the EMEND core crew for their help with specimen collecting and logistics in the field. We also thank personal of the CEF (centre d'étude de la forêt), Jenna Jacobs, Simon Paradis, Dave Gervais and Annie Hibbert for help with writing and development of ideas

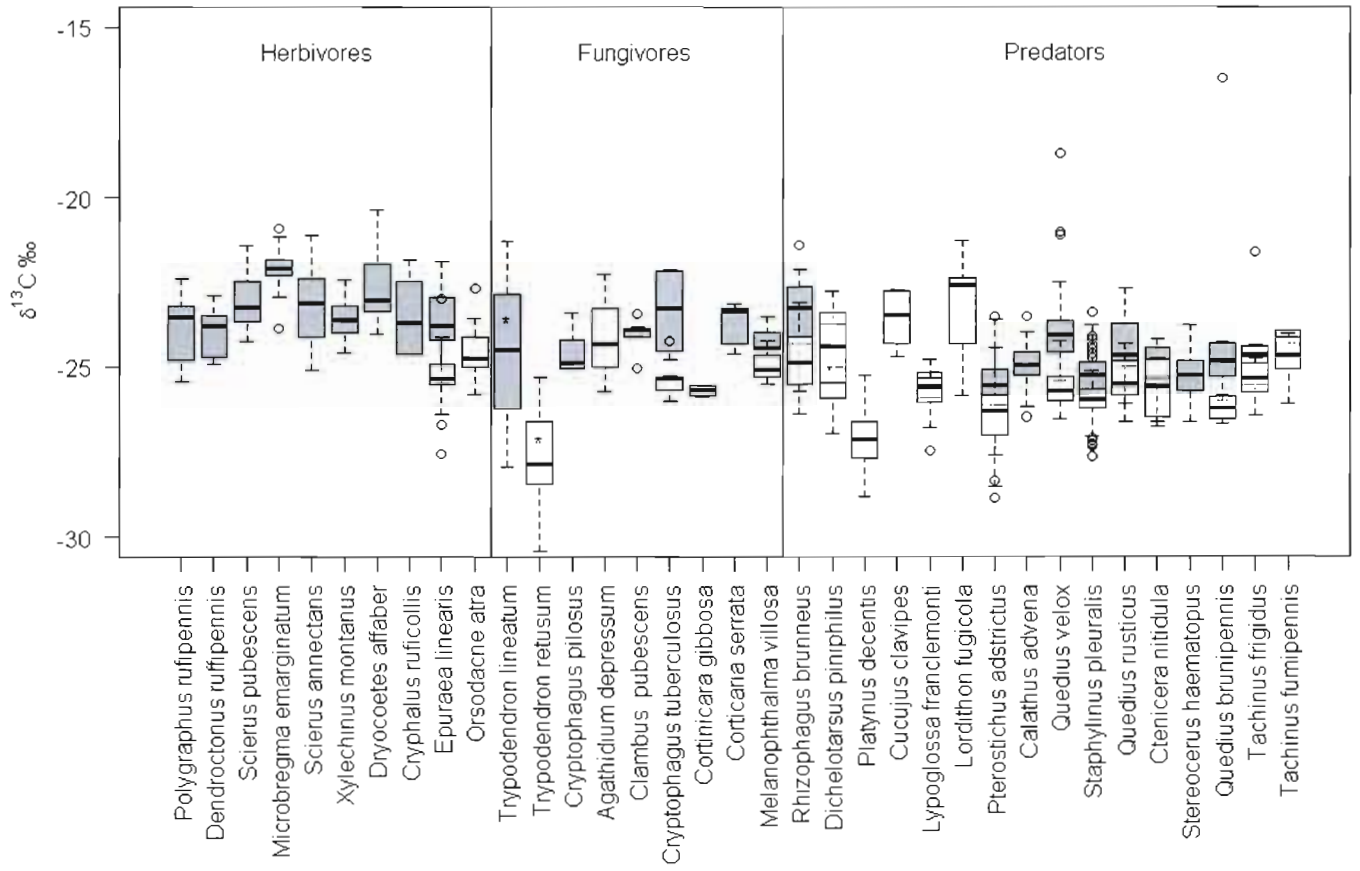

Figure 2.1. Box plots showing $\delta^{13}C$ according species. Grey boxes represent beetles collected in conifer stands and white boxes represent beetles collected in deciduous stands. . Bold line correspond to median observations, boundaries of boxes indicate the 25% and 75% quantile and whiskers to 95%. * indicate ambrosia beetles. Note that light gray areas are created when the white and gray bars overlap.

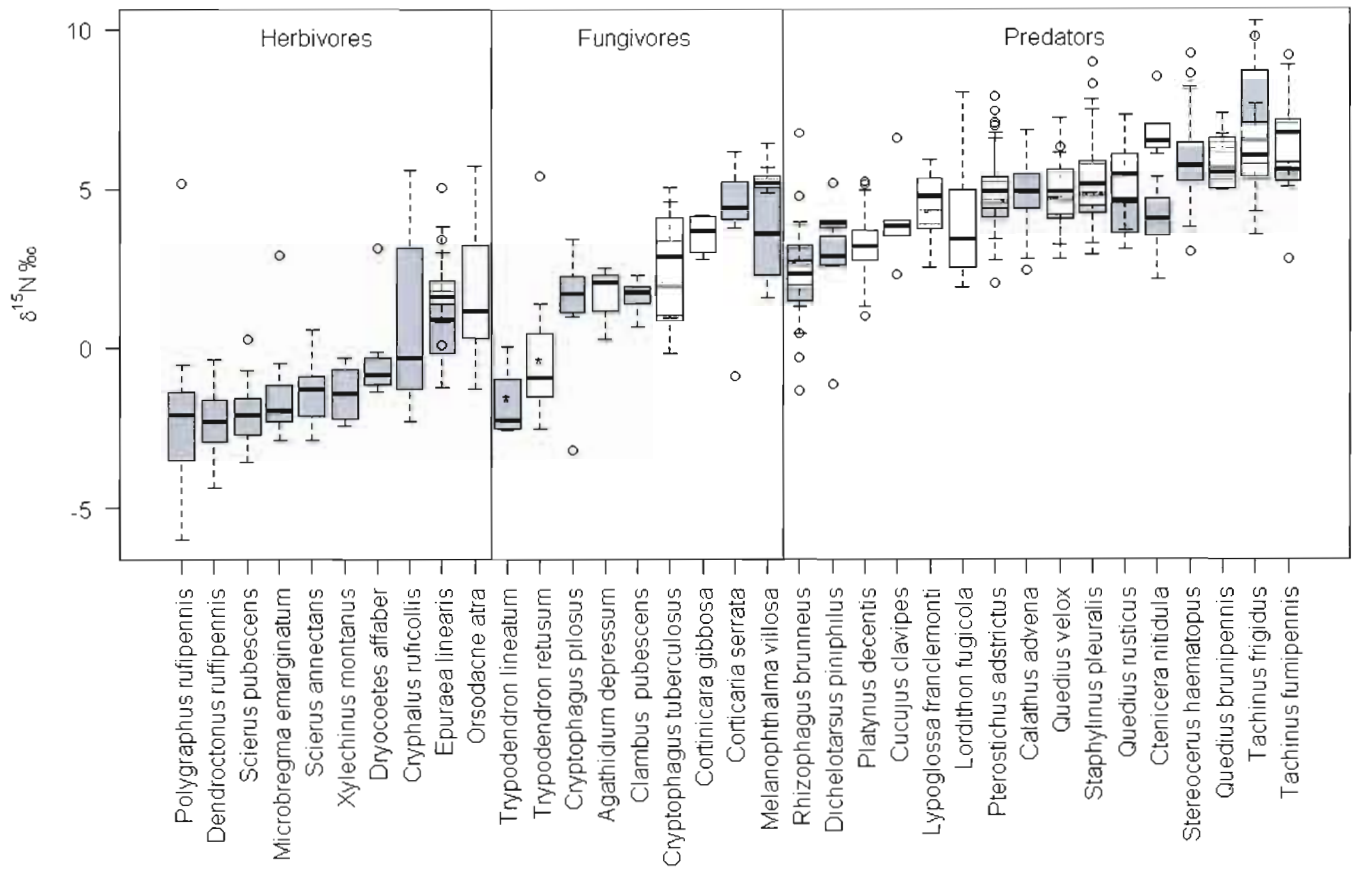

Figure 2.2. Box plots showing $\delta^{15}N$ according species. Grey boxes represent beetles collected in conifer stands and white boxes represent beetles collected in deciduous stands. Bold line correspond to median observations, boundaries of boxes indicate the 25% and 75% quantile and whiskers to 95%. * indicate ambrosia beetles. Note that light gray areas are created when the white and gray bars overlap.

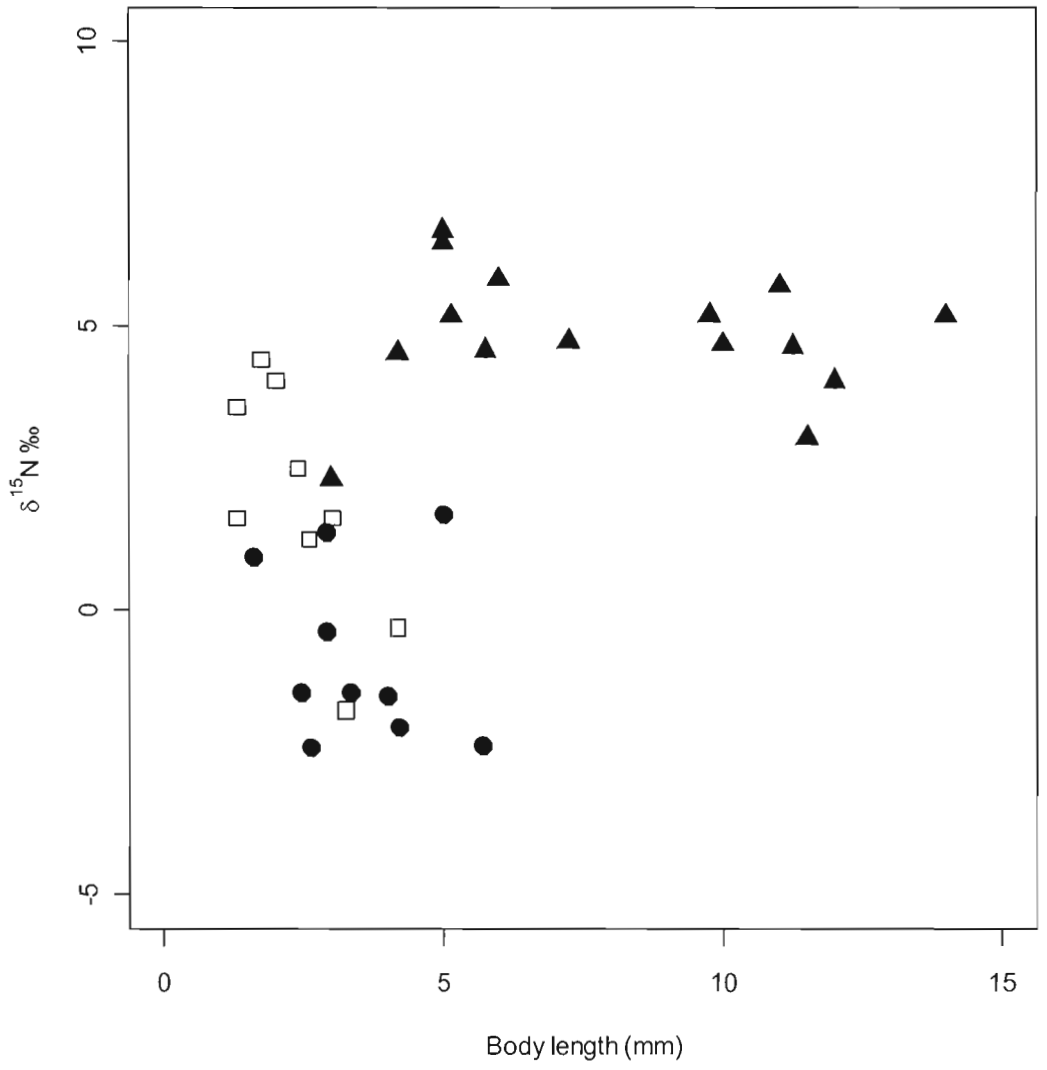

Figure 2.3. Species mean $\delta^{15}N$ (‰) as a function of body length (mm).
Triangles, squares and circles respectivelly represent predators, fungivores and herbivores. Light squares indicate fungivores, black triangles indicate predators and black dots indicate herbivores.

Table 2.1. T-test results with cover type $\delta^{13}C$ and $\delta^{15}N$ means.

	Cover type $\delta^{13}C$ means and t test statistics					Cover type $\delta^{15}N$ means and t test statistics				
	CDOM	DDOM	t	df	p value	CDOM	DDOM	t	df	p value
Epuraea linearis	-23.708	-25.290	4.229	28.355	**0.0002**	1.022	1.757	-1.528	21.615	0.1411
Cryptophagus tuberculosus	-23.367	-25.370	2.791	3.587	0.0558	2.107	2.721	-0.524	5.751	0.6201
Melanophthalma villosa	-24.241	-24.962	1.629	3.629	0.1859	3.802	5.236	-1.369	3.286	0.2571
Rhizophagus brunneus	-23.492	-24.635	2.860	26.646	**0.0081**	2.391	2.272	0.250	31.428	0.8040
Dichelotarsus piniphilus	-24.900	-24.440	-0.395	1.536	0.7407	2.745	3.905	-1.794	7.351	0.1139
Lypoglossa franclemonti	-25.545	-25.775	0.566	1.336	0.6516	4.286	4.548	-0.588	1.549	0.6307
Pterostichus adstrictus	-25.697	-26.719	5.709	31.658	< **0.0001**	4.655	4.629	0.076	29.119	0.9403
Quedius velox	-23.821	-25.259	2.752	28.519	**0.0102**	4.553	4.913	-1.045	30.782	0.3043
Staphylinus pleuralis	-25.442	-26.181	4.849	33.125	< **0.0001**	5.205	5.155	0.163	31.976	0.8714
Quedius rusticus	-24.515	-25.407	3.046	20.853	**0.0062**	4.693	5.529	-2.120	24.209	**0.0445**
Ctenicera nitidula	-25.180	-25.655	0.908	8.765	0.3883	3.995	6.870	-4.707	9.430	**0.0010**
Quedius brunipennis	-24.948	-25.058	0.088	7.684	0.9320	5.837	5.803	0.086	11.566	0.9331
Tachinus frigidus	-24.602	-25.412	1.816	14.484	0.0901	6.871	6.410	0.492	13.776	0.6307
Tachinus fumipennis	-24.368	-24.729	0.845	1.322	0.5234	5.593	6.592	-1.789	4.955	0.1342

Table 2.2. Oneway analysis of variance of $\delta^{15}N$ by guilds and $\delta^{15}N$ by species within guilds. Means comparisons for all guild pairs using Tukey-Kramer HSD show guilds are all significantly different.

Source	Df	Sum Sq	Mean Sq	F value	P value
Guild differences					
guild	2	3325.739	1662.87	456.847	< 0.0001
Error	534	1943.696	3.643		
Within guild species differences					
Herbivores species	11	401.426	36.493	13.850	< 0.0001
Error	165	434.768	2.635		
Fungivores species	6	63.005	10.501	3.626	0.0059
Error	39	112.959	2.896		
Predators species	14	447.001	31.929	19.703	< 0.0001
Error	299	484.537	1.621		

Table 2.3. Species $\delta^{15}N$ means and means comparisons for all species pairs using Tukey-Kramer HSD. Species not connected by the same letter are significantly different.

Guilds and species	Tukey code	Mean $\delta^{15}N$ (‰)
Herbivores		
Orsodacne atra	A	1.68
Epuraea linearis	A	1.38
Cryphalus ruficollis	A B	0.95
Dryocoetes affaber	A B C	-0.37
Xylechinus montanus	B C	-1.43
Scierus annectans	C	-1.44
Microbregma emarginatum	C	-1.50
Scierus pubescens	C	-2.05
Dendroctonus ruffipennis	C	-2.36
Polygraphus rufipennis	C	-2.39
Fungivores		
Melanophthalma villosa	A	4.42
Corticaria serrata	A B	4.04
Cortinicara gibbosa	A B	3.58
Cryptophagus tuberculosus	A B	2.50
Clambus pubescens	A B C	1.62
Agathidium depressum	A B C	1.62
Cryptophagus pilosus	B C	1.24
Trypodendron retusum	C	-0.30
Trypodendron lineatum	C	-1.77
Predators		
Tachinus frigidus	A	6.68
Tachinus fumipennis	A B	6.47
Quedius brunipennis	A B C	5.82
Stereocerus haematopus	A B C	5.70
Ctenicera nitidula	A B C	5.19
Quedius rusticus	B C	5.18
Staphylinus pleuralis	B C	5.18
Quedius velox	C	4.73
Calathus advena	B C D E	4.68
Pterostichus adstrictus	C	4.64
Lordithon fugicola	C D E	4.58
Lypoglossa franclemonti	C E	4.53
Cucujus clavipes	C D E F	4.04
Platynus decentis	D F	3.05
Dichelotarsus piniphilus	D E F	2.98
Rhizophagus brunneus	F	2.32

Table 2.4. Linear regressions results showing the effect of size on mean $\delta^{15}N$ of species within each guild.

Source	Estimate	Std. error	t value	Pr(>|t|)	n	R^2
Herbivores						
Intercept	0.1316	1.5015	0.088	0.932		
Length	-0.2464	0.4059	-0.607	0.559	10	0.039
Fungivores						
Intercept	5.6275	1.4085	3.995	**0.005**		
Length	-1.5440	0.5441	-2.838	**0.025**	9	0.535
Predators						
Intercept	5.0512	0.8057	6.269	**<0.001**		
Length	-0.0246	0.0924	-0.266	0.794	16	0.005

2.8 Reference

In order to cut back paper use we provide references for this article at the end of this document along with all other cited references in the thesis.

CONCLUSION GÉNÉRALE

Les effets de l'aménagement écosystémique sur les communautés d'arthropodes en milieux forestiers sont manifestes (Gandhi *et al.*, 2004 ; Jacobs, Work and Spence, 2008 ; Klimaszewski *et al.*, 2005) et les groupes d'arthropodes utilisés à titre de bioindicateurs écologiques constituent un outil important pour l'amélioration des techniques de coupes et la protection de la biodiversité dans un cadre de développement durable (Buddle *et al.*, 2006 ; Lindenmayer, Margules and Botkin, 2000 ; Work *et al.*, 2008). Ainsi, l'ajout de connaissances sur les mécanismes et les facteurs qui expliquent directement la dynamique des communautés observées en milieux perturbés est nécessaire au développement de l'aménagement basé sur les perturbations naturelles. La stabilité des communautés est liée en bonne partie à la stabilité des réseaux trophiques et plusieurs études démontrent que plus les réseaux alimentaires sont complexes et constitués de liens trophiques faibles, plus ils sont stables et résilients suite aux perturbations (Fagan, 1997 ; Romanuk *et al.*, 2006).

Bien que certaines études aient caractérisé la signature isotopique de nombreux groupes d'arthropodes forestiers, notre étude est, à notre connaissance, la première à évaluer l'effet des coupes forestières sur la variabilité isotopique des coléoptères en forêt boréale mixte au niveau de l'espèce. Nos résultats démontrent que les coupes forestières ont peu d'effets sur la variabilité de la diète des coléoptères généralistes et suggèrent que les ressources disponibles sont similaires, quel que soit le traitement. Nous avons détecté des différences de $\delta^{13}C$ entre les types de couverts forestiers, ces disparités isotopiques indiquent que la dispersion chez les espèces de coléoptères que nous avons étudiés est faible et qu'ils ne se déplacent pas beaucoup d'un type de forêt à un autre. Ces disparités isotopiques pourraient être mises à profit afin de déterminer avec précision la dispersion des espèces à la frontière de deux types de milieux. Nous avons également démontré que les niveaux trophiques des espèces de coléoptères ne sont pas influencés par le type de couvert, ceci qui indique que les espèces ne changent pas drastiquement leur diète au fil de la succession végétale et implique que les réponses compensatoires observées après les perturbations ne proviennent pas de changements alimentaires. De plus, en stipulant que les espèces ont évolué avec les perturbations naturelles, l'approche de l'aménagement par filtre brute suggère du même coup qu'il est imporbable que les espèces s'addaptent rapidement à de nouvelles perturbations.

Nous réitérons donc l'importance de la conservation des espèces afin d'assurer un maximum de redondance au niveau des réseaux alimentaires.

Nous devons souligner que la caratérisation de l'ensemble des proies, des prédateurs et des ressources disponibles de l'écosytème était au-delà de la portée d'un projet comme le notre. Ainsi, nous considérons qu'il serait imprudent d'inférer tout lien trophique entre deux espèces sur la seule base de nos résultats. Il est également important de reconnaître les limites de l'utilisation des isotopes stables, malgré le fait que ces derniers puissent révéler plusieurs aspects de la diète d'un organisme, il n'en demeure pas moins que certain aspects méthodologiques compliquent l'interprétation des résultats. Par exemple, les valeurs de fractionnement isotopique varient selon le type d'organime considéré et ne sont pas connu pour l'ensemble des espèces.

Toutefois, la caractérisation des valeurs isotopiques d'un grand nombre d'espèces de coléoptères nous a permis d'établir les bases de la connaissance en ce qui a trait à la signature isotopique de la faune entomologique spécifique au projet EMEND.

Appendix A

Number of specimens measured for each replicate of treatment and cover type for all years per species. Bold characters show replicates with problematic numbers of specimens.

	0			20			100		
	rep 1	rep 2	rep 3	rep 1	rep 2	rep 3	rep 1	rep 2	rep 3
Platynus decentis (DDOM)									
2000	7	7	7	7	7	7	7	7	7
2004	6	3	**0**	**2**	5	**0**	7	**2**	**1**
2007	7	7	5	7	7	7	5	7	7
Stereocerus haematopus (CDOM)									
2000	7	7	7	7	6	6	**1**	6	7
2004	5	**2**	**0**	**2**	5	**0**	6	7	7
2007	**1**	**0**	**0**	7	**1**	2	7	6	3
Pterostichus adstrictus (DDOM)									
2000	7	7	7	7	7	7	6	7	7
2004	6	5	3	3	7	3	7	5	3
2007	2	4	7	**2**	**1**	**2**	5	6	**0**
Pterostichus adstrictus (CDOM)									
2000	7	7	5	7	7	7	3	7	4
2004	7	7	4	7	3	7	6	7	7
2007	3	3	5	6	**1**	5	7	7	7
Staphylinus pleuralis (DDOM)									
2000	7	7	7	7	7	7	7	7	7
2004	**0**	7	**0**	4	7	7	7	7	7
2007	5	7	3	6	6	7	7	7	4
Staphylinus pleuralis (CDOM)									
2000	7	7	7	6	7	7	4	6	7
2004	7	4	**0**	6	7	7	7	7	7
2007	**2**	6	4	7	4	3	6	7	3

BIBLIOGRAPHIE

Albers, D., M. Schaefer and S. Scheu. 2006. Incorporation of plant carbon into the soil animal food web of an arable system. *Ecology*. vol. 87, no 1, p. 235-245.

Alberta Sustainable Resource Development. 2000. 2000 Annual Report: Forest Health in Alberta. In. Department of Sustainable Resource Development, Forestry Division, Forest Management Branch, Forest Health Section., Edmonton.

Alberta Sustainable Resource Development. 2001. 2001 Annual Report: Forest Health in Alberta. In. Department of Sustainable Resource Development, Forestry Division, Forest Management Branch, Forest Health Section., Edmonton.

Alberta Sustainable Resource Development. 2002. 2002 Annual Report: Forest Health in Alberta. In. Department of Sustainable Resource Development, Forestry Division, Forest Management Branch, Forest Health Section., Edmonton.

Alberta Sustainable Resource Development. 2003. 2003 Annual Report: Forest Health in Alberta. In. Department of Sustainable Resource Development, Forestry Division, Forest Management Branch, Forest Health Section., Edmonton.

Armstrong, G. W. 1999. A stochastic characterisation of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management. *Canadian Journal of Forest Research*. vol. 29, no 4, p. 424-433.

Armstrong, G. W., W. L. Adamowicz, J. A. Beck Jr, S. G. Cumming and F. K. A. Schmiegelow. 2003. Coarse filter ecosystem management in a nonequilibrating forest. *Forest Science*. vol. 49, no 2, p. 209-223.

Arnett, R. H. J., and M. C. Thomas. 2001a. *American beetles v. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia.*, 2 t. Boca Raton, Florida: CRC Press. 443 p.

--------. 2001b. *American beetles v. 2. Polyphaga: Scarabaeoidea through Curculionoidea.* Boca Raton, Florida.: CRC Press. 861 p.

Atshusi, M., and Y. Yoshito. 2005. Development of food web analysis using stable isotope ratios in the paddy field aquatic ecosystem. *Transactions of the Japanese Society of Irrigation Drainage & Reclamation Engineering*. vol. 73, no 6, p. 671-680.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. vol. 63, p. 247-300.

Ball, G.E.; Nègre, J. 1972. The taxonomy of the Nearctic species of the genus Calathus Bonelli (Coleoptera: Carabidae:Agonini). *Transactions of the American Entomological Society*. vol 98, p. 412-533.

Ball, G.E.; Nègre, J. 1972. The taxonomy of the Nearctic species of the genus Calathus Bonelli (Coleoptera: Carabidae:Agonini). *Transactions of the American Entomological Society*. vol 98, p. 412-533.

Bennett, P. M., and K. A. Hobson. 2009. Trophic structure of a boreal forest arthropod community revealed by stable isotope (delta C-13, delta N-15) analyses. *Entomological Science*. vol. 12, no 1, p. 17-24.

Bergeron, Y., and P. R. Dansereau. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *Journal of vegetation sciences*. vol. 79, p. 51-63.

Bergeron, Y., and B. Harvey. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. *Forest Ecology and Management*. vol. 92, no 1-3, p. 235-242.

Bergeron, Y., B. Harvey, A. Leduc and S. Gauthier. 1999. Forest management strategies based on the dynamics of natural disturbances - Considerations and a proposal for a model allowing an even-management approach. *Forestry Chronicle*. vol. 75, no 1, p. 55-61.

Bird, S. B., R. N. Coulson and R. R. Fisher. 2004. Changes in soil and litter arthropod abundance following tree harvesting and site preparation in a loblolly pine (*Pinus taeda* L.) plantation. *Forest Ecology and Management*. vol. 202, no 1-3, p. 195-208.

Blüthgen, N., G. Gebauer and K. Fiedler. 2003. Disentangling a rainforest food web using stable isotopes: Dietary diversity in a species-rich ant community. *Oecologia*. vol. 137, no 3, p. 426-435.

Bourgeois, L., D. Kneeshaw, L. Imbeau, N. Bélanger, S. Yamasaki and S. Brais. 2007. How do Alberta's, Ontario's and Quebec's forest operation laws respect ecological sustainable forest management criteria in the boreal forest? *Forestry Chronicle*. vol. 83, no 1, p. 61-71.

Bousquet,Y. 1990. A review of the North American species of Rhizophagus Herbst Ani. A revision of the nearctic members of the subgenus anomophagus Reitter (Coleoptera: Rhizophagidae). *Canadian Entomologist*. vol 122, 131-171.

Bright, D., E. J. 1976. *The bark beetles of Canada and Alaska (Coleoptera: Scolytidae)*. Coll. «The insects and arachnids of Canada and Alaska. Part 2. ». Ottawa, Canada. 241 p.

Brooks, A.R. 1960. Adult Elateridae of Southern Alberta, Saskatchewan and Manitoba (Coleoptera). The Canadian Entomologist supplement 20 Vol. XCII.

Brooks, J. R., L. B. Flanagan, N. Buchmann and J. R. Ehleringer. 1997. Carbon isotope composition of boreal plants: Functional grouping of life forms. *Oecologia*. vol. 110, no 3, p. 301-311.

Bennett, P. M., and K. A. Hobson. 2009. Trophic structure of a boreal forest arthropod community revealed by stable isotope (delta C-13, delta N-15) analyses. *Entomological Science*. vol. 12, no 1, p. 17-24.

Bergeron, Y., and P. R. Dansereau. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *Journal of vegetation sciences*. vol. 79, p. 51-63.

Bergeron, Y., and B. Harvey. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. *Forest Ecology and Management*. vol. 92, no 1-3, p. 235-242.

Bergeron, Y., B. Harvey, A. Leduc and S. Gauthier. 1999. Forest management strategies based on the dynamics of natural disturbances - Considerations and a proposal for a model allowing an even-management approach. *Forestry Chronicle*. vol. 75, no 1, p. 55-61.

Bird, S. B., R. N. Coulson and R. R. Fisher. 2004. Changes in soil and litter arthropod abundance following tree harvesting and site preparation in a loblolly pine (*Pinus taeda* L.) plantation. *Forest Ecology and Management*. vol. 202, no 1-3, p. 195-208.

Blüthgen, N., G. Gebauer and K. Fiedler. 2003. Disentangling a rainforest food web using stable isotopes: Dietary diversity in a species-rich ant community. *Oecologia*. vol. 137, no 3, p. 426-435.

Bourgeois, L., D. Kneeshaw, L. Imbeau, N. Bélanger, S. Yamasaki and S. Brais. 2007. How do Alberta's, Ontario's and Quebec's forest operation laws respect ecological sustainable forest management criteria in the boreal forest? *Forestry Chronicle*. vol. 83, no 1, p. 61-71.

Bousquet,Y. 1990. A review of the North American species of Rhizophagus Herbst Ani. A revision of the nearctic members of the subgenus anomophagus Reitter (Coleoptera: Rhizophagidae). *Canadian Entomologist*. vol 122, 131-171.

Bright, D., E. J. 1976. *The bark beetles of Canada and Alaska (Coleoptera: Scolytidae)*. Coll. «The insects and arachnids of Canada and Alaska. Part 2. ». Ottawa, Canada. 241 p.

Brooks, A.R. 1960. Adult Elateridae of Southern Alberta, Saskatchewan and Manitoba (Coleoptera). The Canadian Entomologist supplement 20 Vol. XCII.

Brooks, J. R., L. B. Flanagan, N. Buchmann and J. R. Ehleringer. 1997. Carbon isotope composition of boreal plants: Functional grouping of life forms. *Oecologia*. vol. 110, no 3, p. 301-311.

Buddle, C. M., D. W. Langor, G. R. Pohl and J. R. Spence. 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. *Biological Conservation*. vol. 128, no 3, p. 346-357.

Bunnell, F. L., L. L. Kremsater and E. Wind. 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: Relationships within stands. *Environmental Reviews*. vol. 7, no 3, p. 97-146.

Caldarelli, G., P. G. Higgs and A. J. McKane. 1998. Modelling coevolution in multispecies communities. *Journal of Theoretical Biology*. vol. 193, no 2, p. 345-358.

Cambell, J.M. 1973.A revision of the genus *Tachinus* (Coleoptera: Staphylinidae) of North and Central America. Memoirs of the Entomological Society of Canada No. 90. 137 p.

Campbell, J.M. 1982. A revision of the genus *Lordithon* Thomson of North and Central America (Coleoptera: Staphylinidae). Memoirs of the Entomological Society of Canada No. 119. 114 p.

Chahartaghi, M., R. Langel, S. Scheu and L. Ruess. 2005. Feeding guilds in Collembola based on nitrogen stable isotope ratios. *Soil Biology & Biochemistry*. vol. 37, no 9, p. 1718-1725.

Cohen, J. E. 1989. Ecology - Just proportions in food webs. *Nature*. vol. 341, no 6238, p. 104-105.

Cohen, J. E., S. L. Pimm, P. Yodzis and J. Saldana. 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*. vol. 62, no 1, p. 67-78.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*. vol. 42, no 5, p. 495-506.

Deniro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*. vol. 45, no 3, p. 341-351.

Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*. vol. 84, no 10, p. 2522-2531.

Drapeau, P., A. Leduc, Y. Bergeron, S. Gauthier and J. P. Savard. 2003. Bird communities in old lichen-black spruce stands in the clay belt: Problems and solutions regarding forest management. *Forestry Chronicle*. vol. 79, no 3, p. 531-540.

Drossel, B., P. G. Higgs and A. J. McKane. 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. *Journal of Theoretical Biology*. vol. 208, no 1, p. 91-107.

Eggers, T., and T. H. Jones. 2000. You are what you eat...or are you? *Trends in Ecology and Evolution*. vol. 15, no 7, p. 265-266.

Elton, C. 1927. *Animal Ecology*. London: Sidgwick & Jackson, Ltd.

Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. *American Naturalist*. vol. 150, no 5, p. 554-567.

Fagan, W. F., E. Siemann, C. Mitter, R. F. Denno, A. F. Huberty, H. A. Woods and J. J. Elser. 2002. Nitrogen in insects: Implications for trophic complexity and species diversification. *American Naturalist*. vol. 160, no 6, p. 784-802.

Fall, H.C. 1899. Revision of the Lathridiidae of Boreal America. *Transactions of the American Entomological Society*, vol 36. p. 101-192.

Fall, H.C. 1933. A review of the north American species of agathidium (Coleoptera: Silphidae). *Entomologica Americana*. vol 14, no 3. p. 99-131.

Fry, B. 2006. *Stable Isotope Ecology*. New York: Springer. 297 p.

Gandhi, K. J. K., J. R. Spence, D. W. Langor and L. E. Morgantini. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biological onservation*. vol. 102, no 2, p. 131-141.

Gandhi, K. J. K., J. R. Spence, D. W. Langor, L. E. Morgantini and K. J. Cryer. 2004. Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in northern coniferous forests. *Canadian Journal of Forest Research*. vol. 34, no 6, p. 1319-1331.

Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. *Annales Zoologici Fennici*. vol. 31, no 1, p. 203-217.

Hairston, N. G. 1993. Cause-effect relationships in energy-flow, trophic structure, and interspecific interactions. *American Naturalist*. vol. 142, no 3, p. 379-411.

Halaj, J., R. W. Peck and C. G. Niwa. 2005. Trophic structure of a macroarthropod litter food web in managed coniferous forest stands: A stable isotope analysis with δ15N and δ13C. *Pedobiologia*. vol. 49, no 2, p. 109-118.

Hamilton, S. K., J. L. Tank, D. F. Raikow, E. R. Siler, N. J. Dorn and N. E. Leonard. 2004. The role of instream vs allochthonous N in stream food webs: modeling the results of an isotope addition experiment. *Journal of the North American Benthological Society*. vol. 23, no 3, p. 429-448.

Hammond, J., H. E, D. Langor and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). *Canadian Journal of Forest Research*. vol. 31, p. 1175-1183.

Hammond, P.M. and J. F. Lawrence. 1989."Appendix: mycophagy in insects: a summary". In: *Insect-fungus interactions*, Eds., N.Wilding, N.M. Colling, P.M. Hammond and J.F. Webber, 14th Symposium of the Royal Entomological Society of London in collaboration with the British Mycological Society, Academic Press, London. p. 344.

--------. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Canadian Journal of Forest Research*, no 34, p. 1-39.

Hannam, K. D., S. A. Quideau and B. E. Kishchuk. 2007. The microbial communities of aspen and spruce forest floors are resistant to changes in litter inputs and microclimate. *Applied Soil Ecology*. vol. 35, no 3, p. 635-647.

Hansen, A. J., T. A. Spies, F. J. Swanson and J. L. Ohmann. 1991. Conserving biodiversity in managed forests - lessons from natural forests. *Bioscience*. vol. 41, p. 381-392.

Hansson, L.-A., and L. J. Tranvik. 2003. Food webs in sub-Antarctic lakes: A stable isotope approach. *Polar Biology*. vol. 26, no 12, p. 783-788.

Haubert, D., R. Langel, S. Scheu and L. Ruess. 2005. Effects of food quality, starvation and life stage on stable isotope fractionation in Collembola. *Pedobiologia*. vol. 43, no 3, p. 229-237.

Heliola, J., M. Koivula and J. Niemela. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. *Conservation Biology*. vol. 15, no 2, p. 370-377.

Hishi, T., F. Hyodo, S. Saitoh and H. Takeda. 2007. The feeding habits of Collembola along decomposition gradients using stable carbon and nitrogen isotope analyses. *Soil Biology & Biochemistry*. vol. 39, no 7, p. 1820-1823.

Hoebeke, E.R. 1992. Taxonomy and distribution of the athetine genus Lypoglossa Fenyes (Coleoptera: Staphylinidae: Aleocharinae) in North America, with description of a new species. *Journal of the New York Entomological Society*, vol 100, p. 381-398.

Holliday, N. J. 1991. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. *Canadian Entomologist*. vol. 123, no 6, p. 1369-1389.

--------. 1992. The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. *Canadian Journal of Zoology*. vol. 70, no 3, p. 440-452.

Holyoak, M., and S. Sachdev. 1998. Omnivory and the stability of simple food webs. *Oecologia*. vol. 117, no 3, p. 413-419.

Hunter, M. L. 1993. Natural fire regimes as a spacial model for managing boreal forest. *Biological Conservation*. vol. 65, p. 115-120.

Hunter, M. L. J., J. G. L. Jacobson and T. Webb. 1988. Paleoecology and the Coarse-Filter Approach to Maintaining Biological Diversity. *Conservation Biology*. vol. 2, no 4, p. 375-385.

Jacobs, J. M., J. R. Spence and D. W. Langor. 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. *Agricultural and Forest Entomology*. vol. 9, no 1, p. 3-16.

Jacobs, J. M., T. T. Work and J. R. Spence. 2008. *In Back to the Roots or Back to the Future? Towards a New Synthesis between Taxonomic, Ecological and Biogeographical Approaches in Carabidology, Proceedings of the XIII European Carabidologists Meeting, Blagoevgrad, Bulgaria, August 20-24 2007*. (Bulgaria). L. Penev, T Erwin and T. Assmann Pensoft Publishers, p. 425-450.

Jansen, V. A. A., and G. D. Kokkoris. 2003. Complexity and stability revisited. *Ecology Letters*. vol. 6, no 6, p. 498-502.

Kasantsev, S. 1992. Contribution to the knowledge of Palaearctic Cantharidae (Coleoptera). Notes on Dichelotarsus Motschulsky. *Entomologica Basiliensia*, vol. 15, p. 267-277.

Kishchuk, B. E. 2004. *Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northwestern Alberta. Edmonton, Alberta, Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre*. 136 p.

Klimaszewski, J., D. W. Langer, T. T. Work, G. Pelletier, H. E. J. Hammond and C. Germain. 2005. The effects of patch harvesting and site preparation on ground beetles (Coleoptera, Carabidae) in yellow birch dominated forests of southeastern Quebec. *Canadian Journal of Forest Research*. vol. 35, no 11, p. 2616-2628.

Koivula, M., J. Kukkonen and J. Niemelä. 2002. Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation*. vol. 11, no 7, p. 1269-1288.

Kupfer, A., R. Langel, S. Scheu, W. Himstedt and M. Maraun. 2006. Trophic ecology of a tropical aquatic and terrestrial food web: Insights from stable isotopes (15N). *Journal of Tropical Ecology*. vol. 22, no 4, p. 469-476.

Langor, D., and J. R. Spence. 2006. Arthropods as ecological indicators of sustainability in Canadian forests. *The Forestry Chronicle*. vol. 82, no 3, p. 344-350.

Larochelle, A., and M.-C. Larivière. 2003. *A Natural History of the Ground Beetles (Coleptera: Carabidae) of America North of Mexico*: Pensoft. 582 pages.

Leschen, R. A.B. 1996. Phylogeny and Revision of the Genera of Cryptophagidae (Coleoptera: Cucujoidea). *The University of Kansas Science bulletin*, vol. 55, No. 15, pp. 549-634.

Lieffers, V. J., R. B. Macmillan, D. MacPherson, K. Branter and J. D. Stewart. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. *Forestry Chronicle*, no 72, p. 286-292.

Lindenmayer, D. B. 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management*. vol. 115, no 2-3, p. 277-287.

Lindenmayer, D. B., C. R. Margules and D. B. Botkin. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology*. vol. 14, no 4, p. 941-950.

Lindo, Z., and S. Visser. 2004. Forest floor microarthropod abundance and oribatid mite (Acari : Oribatida) composition following partial and clear-cut harvesting in the mixedwood boreal forest. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*. vol. 34, no 5, p. 998-1006.

Lindroth, C. H. 1966. The ground beetles (Carabidea, excl.Cincidelinae) of Canada and Alaska. Part 4. *Opuscula Entomologica Supplementum*. vol. 29, p. 409-648.

Loeuille, N., and M. Loreau. 2005. Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*. vol. 102, no 16, p. 5761-5766.

Mabelis, A. 1984. Interference between wood ants and other ant species. *Netherlands Journal of Zoology.*, no 34, p. 1-20.

MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology*. vol. 36, p. 533-536.

Márcio, S. A., I. B. Daniel, M. Glauco, A. G. Ariovaldo and F. d. R. Sérgio. 2007. Using δ13C stable isotopes to quantify individual-level diet variation. *Oecologia*. Vol 152, no 4, p. 643-654

Martikainen, P., J. Kouki and O. Heikkala. 2006. The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera : Carabidae) in boreal pine-dominated forests. *Ecography*. vol. 29, no 5, p. 659-670.

May, R. M. 1971. Stability in multi-species community models. *Mathmatical Biosciences.*, no 12, p. 59-79.

--------. 1973. *Stability and complexity in model ecosystems*. Princeton, N.J.: Princeton University Press. 292 p.

McCann, K., and A. Hastings. 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society - Biological Sciences (Series B)*. vol. 264, no 1385, p. 1249-1254.

McCann, K., A. Hastings and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature*. vol. 395, no 6704, p. 794-798.

McCann, K. S. 2000. The diversity-stability debate. *Nature*. vol. 405, no 6783, p. 228-233.

McGeoch, M. A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*. vol. 73, no 2, p. 181-201.

McLaren, M. A., I. D. Thompson and J. A. Baker. 1998. Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. *Forestry Chronicle*. vol. 74, no 2, p. 241-248.

McNabb, D. M., J. Halaj and D. H. Wise. 2001. Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: A stable isotope analysis. *Pedobiologia*. vol. 45, no 4, p. 289-297.

Memmott, J., N. D. Martinez and J. E. Cohen. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology*. vol. 69, no 1, p. 1-15.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation - variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. *American Naturalist*. vol. 130, no 5, p. 730-757.

Messier, C. 1996. Exploitation de la forêt boréale et conservation de son intégrité écologique : nouvelles approches. In *L'utilisation durable des forêts québécoises: De l'exploitaion à la protection,* p. 135-143. Sainte-Foy, Qué: Les Presses de l'Université Laval.

Minagawa, M., and W. Eitaro. 1984. Stepwise enrichment of 15N along food chains: further evidence and relation between delta 15N and animal age. *Geochimica et Cosmochimica Acta*. vol. 50, p. 2143-2146.

Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. de Ruiter, Q. Dong, A. Hastings, N. C. Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni and D. H. Wall. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters*. vol. 7, no 7, p. 584-600.

Niemela, J. 1997. Invertebrates and boreal forest management. *Conservation Biology*. vol. 11, no 3, p. 601-610.

Niemela, J., D. Langor and J. R. Spence. 1993. Effects of Clear-Cut Harvesting on Boreal Ground-Beetle Assemblages (Coleoptera: Carabidae) in Western Canada. *Conservation Biology*. vol. 7, no 3, p. 551-561.

Nordén, B., T. Appelqvist and B. Olausson. 2002. Diversity, ecology and conservation of wood-inhabiting ascomycetes in Sweden. *Sporsa?cksvampar i do?d ved - ma?ngfald, ekologi och naturva?rdsaspekter*. vol. 96, no 3-4, p. 139-148.

Noss, R. F. 1990. Can we maintain biological and ecological integrity. *Conservation Biology*. vol. 4, no 3, p. 241-243.

--------. 1990. Indicators for monitoring biodiversity - a hierarchical approach. *Conservation Biology*. vol. 4, no 4, p. 355-364.

--------. 1999. Assessing and monitoring forest biodiversity: A suggested framework and indicators. *Forest Ecology and Management*. vol. 115, no 2-3, p. 135-146.

Odum, E. P. (1953). Fundamentals of ecology. Philadelphia, PA:, W. B. Saunders. 574 p.

Oelbermann, K., and S. Scheu. 2002. Stable isotope enrichment (δ15N and δ13C) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): Effects of prey quality. *Oecologia*. vol. 130, no 3, p. 337-344.

Paetzold, A., C. J. Schubert and K. Tockner. 2005. Aquatic terrestrial linkages along a braided-river: Riparian arthropods feeding on aquatic insects. *Ecosystems*. vol. 8, no 7, p. 748-759.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *The Journal of Animal Ecology*. vol. 49, no 3, p. 666-685.

Peterson, B. J., and B. Fry. 1987. Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics*. vol. 18, p. 293-320.

Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature*. vol. 307, no 5949, p. 321-326.

Polis, G. A. 1991. Complex trophic interactions in deserts - an empirical critique of food-web theory. *American Naturalist*. vol. 138, no 1, p. 123-155.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist*. vol. 147, no 3, p. 396-423.

Polis, G. A., and S. McCormick. 1987. Intraguild predation and competition among desert scorpions. *Ecology*, no 68, p. 332-343.

Polis, G. A., C. A. Myers and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*. vol. 20, p. 297-330.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist*. vol. 147, no 5, p. 813-846.

Ponsard, S., and M. Amlou. 1999. Effects of several preservation methods on the isotopic content of Drosophila samples. *Comptes Rendus de l'Academie des Sciences - Serie III*. vol. 322, no 1, p. 35-41.

Ponsard, S., and R. Arditi. 2000. What can stable isotopes (δ15N and δ13C) tell about the food web of soil macro-invertebrates? *Ecology*. vol. 81, no 3, p. 852-864.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*. vol. 83, no 3, p. 703-718.

Pratt, L., and I. Urquhart. 1994. *The Last Great Forest: Japanese Multinationals and Alberta's Northern Forests*. NeWest Press. Edmonton, Alberta. 232 p.

Reichert, S., and A. Cady. 1983. Patterns of resource use and tests for competitive release in a spider community. *Ecology*, no 64, p. 899-913.

Robinson, J. 1987. Mutual predation in assembled communities of odonate species. *Ecology*, no 68, p. 921-927.

Romanuk, T. N., B. E. Beisner, N. D. Martinez and J. Kolasa. 2006. Non-omnivorous generality promotes population stability. *Biology Letters*. vol. 2, no 3, p. 374-377.

Root, R. B. Species diversity and population stability of insect herbivore associated with related host plants in tropical and temperate regions. *Bulletin of the Ecological Society of America*. vol. 62, p. 50.

Sarakinos, H. C., M. L. Johnson and M. J. Vander Zanden. 2002. A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. *Canadian Journal of Zoology*. vol. 80, no 2, p. 381-387.

Scheu, S., and M. Falca. 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. *Oecologia*. vol. 123, no 2, p. 285-296.

Scheu, S., and M. Folger. 2004. Single and mixed diets in Collembola: Effects on reproduction and stable isotope fractionation. *Functional Ecology*. vol. 18, no 1, p. 94-102.

Schulze, E. D., F. S. I. Chapini and G. Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia*. vol. 100, no 4, p. 406-412.

Setälä, H., and T. Aarnio. 2002. Vertical stratification and trophic interactions among organisms of a soil decomposer food web - A field experiment using 15N as a tool. *European Journal of Soil Biology*. vol. 38, no 1, p. 29-34.

Setälä, H., J. Haimi and A. Siira-Pietikäinen. 2000. Sensitivity of soil processes northern forest soils: Are management practices a threat? *Forest Ecology and Management*. vol. 133, no 1-2, p. 5-11.

Shaw, C. H., H. Lundkvist, A. Moldenke and J. R. Boyle. 1991. The relationships of soil fauna to long-term forest productivity in temperate and boreal ecosystems: processes and research strategies. FRI Bulletin. W.J. Dyck and C.A. Mees. Rotorua, NZ,, For. Res. Inst.: 39-77 p.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaing Populus tremula: acomparison between Finnish and Russian Karelia. *Scandivanian Journal of Forest Reasearch*. vol. 9, p. 185-191.

Smetana, A. 1971. Revision of the tribe Quediini of America north of Mexico (Coleoptera: Staphylinidae). Memoirs of the Entomological Society of Canada No. 79. 303 p.

Spence, J. R. 2001. The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology & Evolution*. vol. 16, no 11. p. 591-593.

Spence, J. R.., and W. J. A. Volney. 1999. EMEND Ecosystem Management Emulating Natural Disturbance, Sustainable Forest Management Network Project Report.

Summerville, K. S., and T. O. Crist. 2002. Effects of timber harvest on forest Lepidoptera: Community, guild, and species responses. *Ecological Applications*. vol. 12, no 3, p. 820-835.

Takahashi, K., and Y. Miyajima. 2008. Relationships between leaf life span, leaf mass per area, and leaf nitrogen cause different altitudinal changes in leaf ?13C between deciduous and evergreen species. *Botany*. vol. 86, no 11, p. 1233-1241.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology*. vol. 80, no 5, p. 1455-1474.

Trudell, S. A., P. T. Rygiewicz and R. L. Edmonds. 2004. Patterns of nitrogen and carbon stable isotope ratios in macrofungi, plants and soils in two old-growth conifer forests. *New Phytologist*. vol. 164, no 2, p. 317-335.

Vadeboncoeur, Y., K. S. McCann, M. J. V. Zanden and J. B. Rasmussen. 2005. Effects of multi-chain omnivory on the strength of trophic control in lakes. *Ecosystems*. vol. 8, no 6, p. 682-693.

Warren, P. H., and J. H. Lawton. 1987. Invertebrate predator-prey body size relationships - an explanation for upper-triangular food webs and patterns in food web structure. *Oecologia*. vol. 74, no 2, p. 231-235.

Wise, D. H., D. M. Moldenhauer and J. Halaj. 2006. Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*. vol. 16, no 3, p. 865-876.

Work, T. T., J. M. Jacobs, J. R. Spence and W. J. A. Volney. 2010. High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests. *Ecological Applications*. vol. 20, no 3, p. 741-751.

Work, T. T., M. Koivula, J. Klimaszewski, D. Langor, J. Spence, J. Sweeney and C. Hebert. 2008. 393-414 p.

Work, T. T., D. P. Shorthoude, J. R. Spence, W. J. A. Volney and D. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropod of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwstern Alberta. *Canadian Journal of Forest Research*. vol. 34, p. 417-430.

Yodzis, P. 1989. *Intoduction to theoretical ecology*. New York, USA: Harper and Rowe. 383 p.

Younga-Endrody, S. 1981.The American species of the Familia Clambidae (Coleoptera: Eucinetoidea). Entomologia Generalis 7 (1): 033-067.